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STUDIES ON THE BEHAVIOUR OF ANOMALA OPACICOLLIS (PÉR).

A THESIS PRESENTED FOR THE

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I. INTRODUCTION

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Anomala opacicollis (Pér) is widespread in the "sandveld" areas of Southern Rhodesia. In company with Melolonthid and other Rutelid species it constitutes a serious problem to tobacco growers since the larvae ("whitegrubs" or "manure-worms") which live in the soil, attack tobacco plants. The study of the behaviour of whitegrubs and the adult "chafer beetles" has, therefore, an economic importance, and cultural methods, which avoid attack by these insects, can be devised once their behaviour is understood.

At the Trelawney station of the Tobacco Research Board of Southern Rhodesia, where the following work was carried out, A. opacicollis was found to be the predominant species of whitegrub. Behaviour experiments were therefore conducted on this species, but when other Rutelid species were included in experiments, they did not exhibit any major differences in the behaviour patterns.

II. LIFE HISTORY

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Mitchell (1946, a) summarised the facts known about whitegrubs in Southern Rhodesia in 1946. No work appears to have been published on their behaviour and life history in Rhodesia previously. In the following account, those points which were mentioned by Mitchell are indicated as such, but otherwise the observations are original.

The life history of all Anomala spp. in Southern Rhodesian sandveld areas are similar,(Mitchell,1946 a). The beetles emerge from the soil with the first rains of the wet season, which usually fall sometime in September (Mitchell,1946 a). They fly at night and feed on various indigenous trees (Mitchell, 1946 a). The sexes fly in roughly equal numbers. No economic damage to the foliage of ornamental trees and shrubs has been reported, but these may be eaten as well. Activity continues for some three or four hours after sundown, during which time the beetles are strongly attracted to artificial lights. By daytime, the beetles have burrowed back into the soil and here they remain inactive until the following evening (Mitchell, 1946 a). When dug up from the soil, they do not attempt to fly, preferring to burrow back into the soil or conceal themselves in some other way. The burrow is not extensive and beetles are normally found some 3 or 4 inches below soil surface.

In captivity, eggs are scattered by the female throughout loose soil, but, under natural conditions, where the soil is more less compacted, it is probable that any eggs laid in one day are placed together in the burrow. A. opacicollis females captured a few days after flight activity had begun in October 1951, laid in two or three days 9 to 15 eggs within a week of capture.

The average for 27 females was 13 eggs; no more had been laid when the beetles finally died in mid-December.

At room temperatures of 65 - 75°F, the incubation period of eggs was about 1 month and the 1st and 2nd stadia both appeared to last about 2 weeks. These stages are found in the soil at 3-6" where temperatures fluctuate considerably, rising to 90°F in the hottest part of the day and falling below 60°F at night. However, Mitchell (1946 a,b) reports that in 1945, egglaying of chafer beetles in the field was at a maximum at the beginning of November while 3rd instar larvae began to be numerous at Christmas. This is a period of some seven to eight weeks and is in agreement with the laboratory data.

There are only three larval instars and all feed on living or decaying plant material in the soil (Mitchell, 1946 a). In the veld, the abundant supply of grassroots appears to be an important source of food. The first two instars are too small to cause any appreciable damage to crops, but the third instar can seriously damage tobacco which has not been in the land for more than five weeks (Mitchell, 1946 a).

The 3rd instar larvae feed voraciously for some three to four weeks; the period of severe attack on tobacco from the whole population in the field lasting some five weeks (Mitchell, 1946 a). When fully fed, the larvae become quiescent (Mitchell, 1946 a). These "prepupae" can be distinguished from the active larvae since the gut of the latter always contains faecal matter which is voided in passing into the prepupal stage. In active whitegrubs, the bluish-black contents of the gut can be clearly observed, while prepupae are a uniform yellowish-white colour.

By/

By the end of January most of the larvae have become prepupae (Mitchell, 1946 a). These burrow deeper into the soil, being normally found about 1 foot below soil surface. Here they remain in a weakly-made cell, which is no more than an ovoid space, smoothed inside with saliva. The walls are not formed of cemented soil particles in the true sense and are easily broken.

Pupation occurs the following August or September. It is not known whether the duration of the prepupal stage is determined by prevailing temperatures, or whether it is terminated by some definite stimulus, but once pupation has occurred, the beetle emerges some 15 days later. The life-cycle of Anomala opacicollis invariably occupies one year only, and the other Rutelids occurring with it are similar in this respect (Mitchell, 1946 a).

The beetles do not become active immediately, but remain quiescent in the cell. At this stage, even when dug up, they remain inactive and do not attempt to burrow back into the soil or hide. When placed on exposed soil, they remain there even though they may die from desiccation in hot, dry weather or be attacked by other insects. In the laboratory, this inactive period did not appear to be influenced by temperature nor by soil moisture provided this was kept constant. If, however, the soil was moistened at anytime, the beetles became active the following evening. This is in agreement with field observations that flight begins with the first showers of the season.

III. BEHAVIOUR OF THE ADULT/

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1. TIME OF FLIGHT

Apart from the observation that soil moistening is the stimulus required to make emergent beetles active, little is known about the influence of weather on beetle flights. After a period of drought, rainfall will normally bring out a larger flight than usual, while no flights occur in rainy or thundery weather. Unfortunately, the one season that a light trap was operated to record catches and compare them with meteorological data, flight activity was abnormally low, and no useful information was obtained. Attraction to domestic light begins just after sundown, reaches a maximum between two and four hours after sundown and falls off during the next two hours. Few beetles are found near lights after midnight.

2. FEEDING PREFERENCES

Mitchell (1946 a) remarks that chafer beetles in Southern Rhodesia are particularly attracted to the spring regrowth from roots of a number of indigenous trees, notably muNondo (Isoberlinea globiflora), iMasasa (Brachystegia spiciformis) and muFuti (B.boehmii). However, night observations found these beetles (Adoretus and Schyzonycha spp. as well as Anomala spp.) feeding on all portions of favoured trees and new growth does not, at any rate, form the only part of their diet.

To determine feeding preferences more exactly, the foliage from sixteen common trees were fed to Anomala opacicollis beetles enclosed in glass jars. Batches of four beetles were enclosed in 2 lb. preserving jars containing 2" of moist earth. MuFuti leaves were placed in the jars and left for some days, after which time the areas of leaf eaten were traced onto squared paper and measured. The average area eaten by four beetles in four days was found to be 2.84 square inches, no recording being less than 2 square inches. The leaves of the various test trees, including muFuti, were then placed in the jars and after a further four days the amounts eaten determined. Table 1 gives the results adjusted for differences in the muFuti eaten initially Finally, further muFuti was placed in the jars to observe whether any beetles had been adversely affected by the test. This did not appear to have happened, since the final muFuti was readily eaten in all cases. Although the sixteen trees tested did not comprise all the trees in the area, they represented all the common species and it is unlikely that any major food source was overlooked.

Other/

Other chafer beetles have been recorded as having somewhat different food preferences to Anomala opacicollis, but muFuti, iMasasa and muNondo appear to be attractive to all the indigenous Melolonthidae and Rutelidae. Since these trees are widespread in the sandveld areas, it is unlikely that the food sources of the adult are a limiting factor in the distribution of these insects.

TABLE 1. - Areas of leaves eaten by four Anomala opacicollis beetles in four days.

Tree	Local native name	Area eaten (in^2) (adjusted)
Brachystegia boehmii	muFuti	2.84
Ficus capensis	muKuyu	2.66
Piliostigma thonningii	muTukutu	1.20
Isoberlinea globiflora	muNondo	1.12
Brachystegia spiciformis	iMasasa	1.00
Diplorhynchus mossambicensis	muTowa	1.00
Burkea africana	muKarati	0.61
Sysygium guineense	muKute	0.39
Ormocarpum kirkii	Purpuru	0.35
Pseudolachnosylis maprouneifolia	muTsontsowa	0.04
Terminalia rhodesica	muKonono	0.03
Thespesia garkeana	muMinu	0.01
Vangueriopsis lanciflora	muTufu	0.01
Monotes glaber	muWara	Nil
Heeria reticulata	muHacha	Nil

3. OVIPOSITION

The soil types in which the female beetle prefers to lay her eggs will be related to the sites likely to be infested with whitegrubs. To examine the preferences of A.opacicollis in this respect, the following experiment was done.

A four foot high gauze cage was built over six "plots" of soil isolated from one another and from the surrounding soil by concrete "floors" and sides. The plots, which measured 1 foot deep and 2½ yards by 1 yard in area, were filled in August 1952 with topsoil taken from a tobacco land. This soil was carefully sieved to remove any insects present and then treated to simulate various soil conditions found in the field. In September, A. opacicollis beetles were dug up from the soil and distributed evenly between the caged plots. To ensure further that the cage area was populated by beetles, any caught during the flight period were also distributed within it. Fresh shoots of muFuti were evenly distributed between the plots every evening until mid-November to ensure an even distribution of food material for the beetles. Finally, at the beginning of the following February, the plots were excavated and the numbers of larvae present recorded. Since the plots were filled in August, before the egg-laying had begun, neither eggs nor young larvae could have been introduced with the soil, and all larvae present must have hatched from eggs laid by the beetles introduced into the cage. Table 2 gives the results of the experiment. A small minority of other Anomala species had been introduced with the A.opacicollis beetles, but the great majority of the larvae recovered were A. opacicollis. The foreign species was distributed between the plots in the same proportion as the majority.

TABLE 2. - Soil Preferences of ovipositing A.opacicollis beetles.

Type of plot	Grubs found
1. Natural veld vegetation	86
2. Bare, broken manured soil	66
3. Bare, broken unmanured soil	10
4. Weedy, broken unmanured soil	9
5. Bare, compacted, unmanured soil	5
6. Bare, compacted manured soil	1

The beetles showed a decided preference for the natural veld conditions (1) and for broken, manured soil (2) but little for compacted soil, whether normal (5) or manured (6). Since, in the last instance, the manure was mixed with the soil before it was compacted, the compaction appears to be the deciding factor. Nevertheless, the natural veld plot was accurately compacted, and here the plant cover appears to have been the important factor. The weedy plot (4) did not have nearly as heavy a plant cover and simulated a ploughed land in which no attempt is made to keep weeds controlled. Thus, it appears, from the results, that keeping a ploughed land clear of weeds would not greatly affect its attractiveness to beetles.

These results have an important bearing on farming practices and will be discussed later in connection with larval behaviour.

IV. BEHAVIOUR OF THE LARVAE

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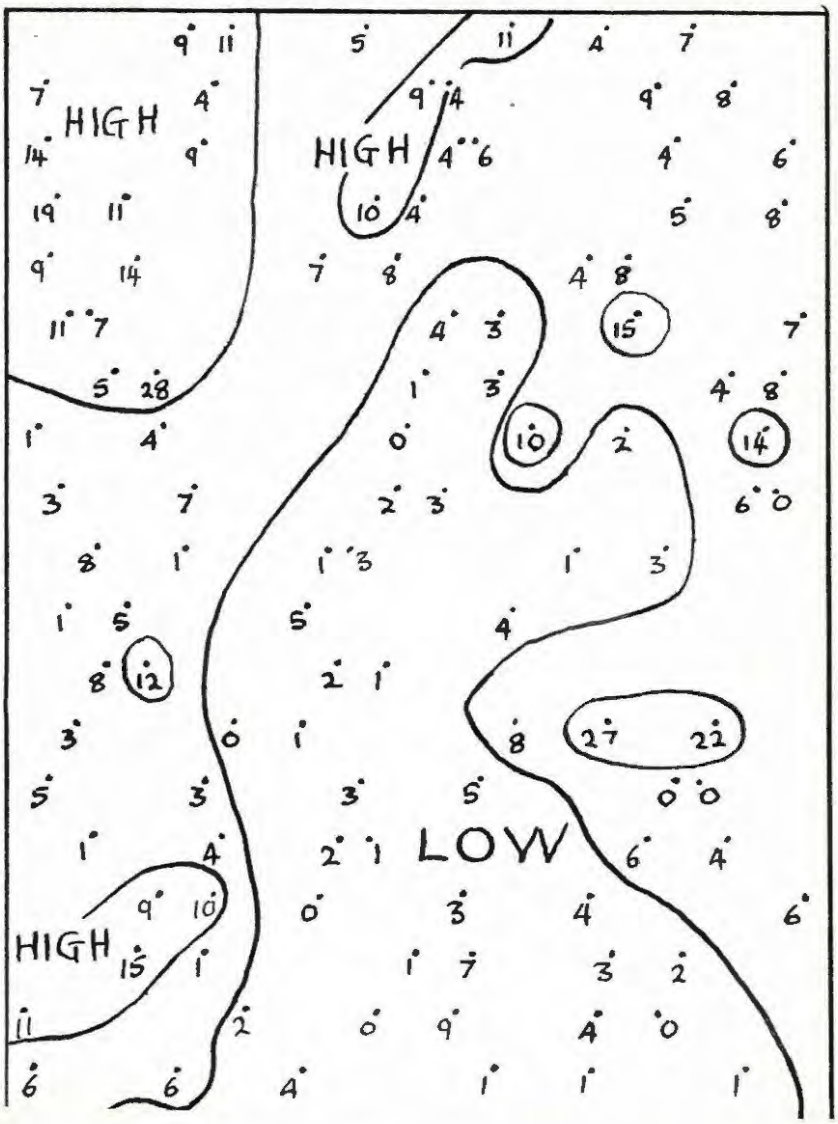
1. LOCAL DISTRIBUTION IN THE SOIL

The distribution of whitegrubs in the soil is erratic. An example of the type of distribution pattern found is given in Figure 1. The land concerned was a 1½ acre field of tobacco grown on a site which had been a cattle kraal for five years previous to cultivation. It contained heavy deposits of manure throughout and was ploughed in August 1952, before the beetle flight period. The field was used for soil insecticide experiments and was planted to tobacco in late December. The tobacco was grown on ridges, 9" high and 3'6" apart and every third ridge was left untreated. To obtain the soil pest distribution data, two 2 foot sections were selected at random in every 54 foot of untreated ridge and were dug away and sieved in early February. The insects recovered were mainly Anomala opacicollis third instar larvae, although other whitegrubs and some Tenebrionid larvae (false wireworms) were also found. Figure 1 gives the distribution of all whitegrubs. In spite of the close proximity of some of the samples, large differences between them occurred and the contours drawn in Figure 1 are only approximations. Nevertheless certain distribution trends are apparent and these will be referred to later.

2. MOVEMENT/

FIGURE 1. - Distribution map of whitegrubs in a ploughed land



2. MOVEMENT IN RELATION TO SOIL FACTORS

The preferences of A. opacicollis larvae in the soil were investigated by placing them in gradients of soil factors and determining their movements. For these experiments, steel troughs, 6 foot long, 6 inches square in cross-section and fitted with air-tight lids were filled with soil in which the desired gradient had been induced. It was seldom possible to establish a continuous gradient, and normally a "step-gradient" was obtained by filling the trough in 6" vertical sections, each section differing from the next. Larvae were buried 1" deep along the length of the trough, either six or twelve per section, and their distribution was then determined after a period of normally a week. Any larvae found dead or on the surface of the soil were ignored.

A. SOIL MOISTURE CONTENT

Water was mixed with dry soil to give soils of desired moisture contents. A trough was filled in 6" sections to give the desired step gradient and the grubs introduced as already described. When the trough was emptied, a week later, the moisture content of each section (per cent dry weight) was obtained from the loss in weight of samples dried in an oven at 100°C. The results using different ranges of moisture content are tabulated in Tables 3 and 4, and graphed in Figures 2 and 3.

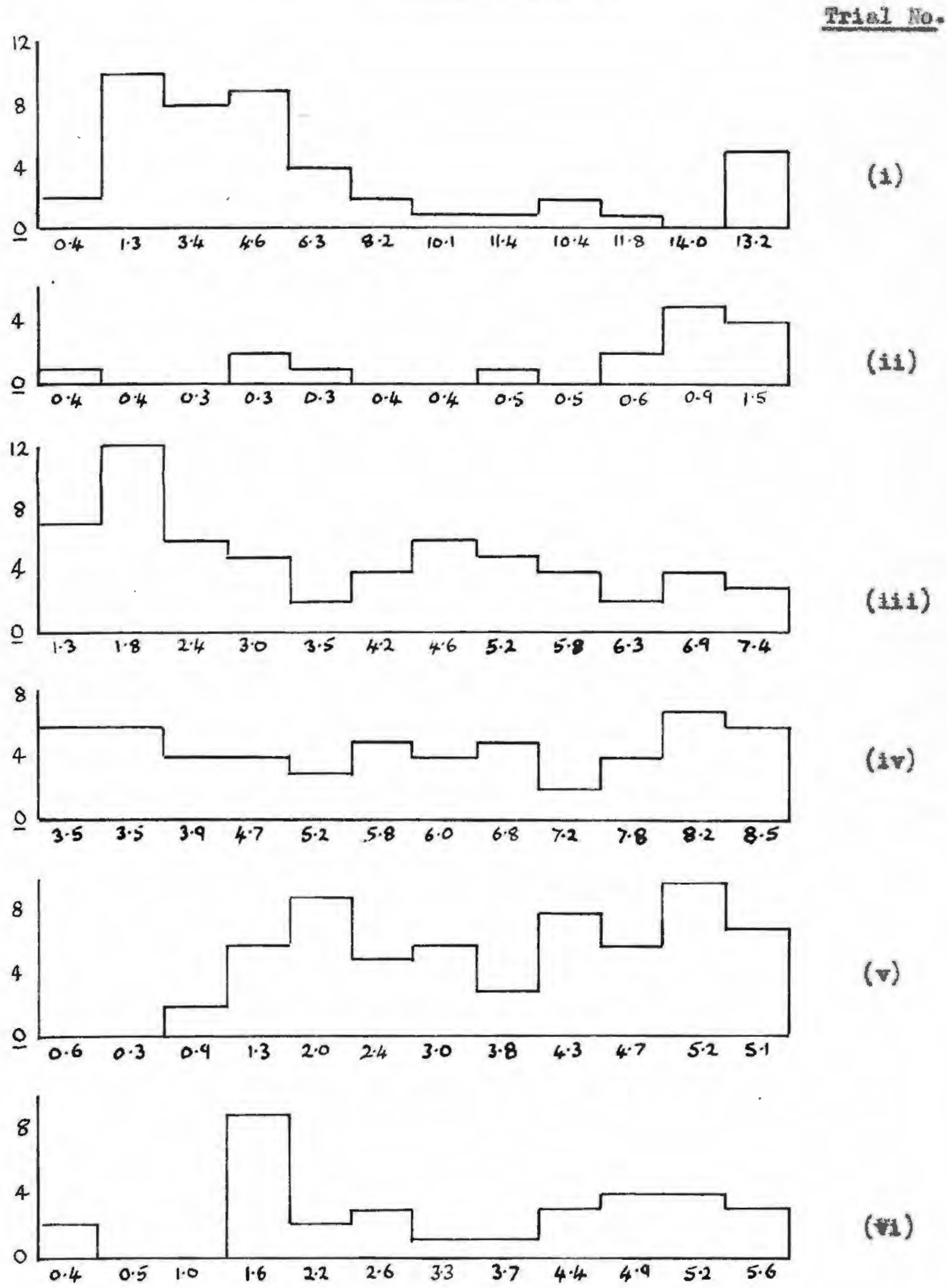
The mean of the peaks in the graphs shown in Figure 3 coincides with approximately 1.7% soil moisture content. This appeared, at first sight, to be a remarkably low value, especially since great difficulty had been found, when keeping whitegrubs under observation, in preventing death due to desiccation.

To/

TABLE 3. - Distribution of *Anomala opacicollis* 3rd instar larvae along soil moisture content Step-gradients.

Trough Section	Trial No.											
	i		ii		iii		iv		v		vi	
	Larvae	M.C.%	Larvae	M.C.%	Larvae	M.C.%	Larvae	M.C.%	Larvae	M.C.%	Larvae	M.C.%
A	2	0.4	1	0.4	7	1.3	6	3.5	0	0.6	2	0.4
B	10	1.3	0	0.4	12	1.8	6	3.5	0	0.3	0	0.5
C	8	3.4	0	0.3	6	2.4	4	3.9	2	0.9	0	1.0
D	9	4.6	2	0.3	5	3.0	4	4.7	6	1.3	9	1.6
E	4	6.3	1	0.3	2	3.5	3	5.2	9	2.0	2	2.2
F	2	8.2	0	0.4	4	4.2	5	5.8	5	2.4	3	2.6
G	1	10.1	0	0.4	6	4.6	4	6.0	6	3.0	1	3.3
H	1	11.4	1	0.5	5	5.2	5	6.8	3	3.8	1	3.7
I	2	10.4	0	0.5	4	5.8	2	7.2	8	4.3	3	4.4
J	1	11.8	2	0.6	2	6.3	4	7.8	6	4.7	4	4.9
K	0	14.0	5	0.9	4	6.9	7	8.2	10	5.2	4	5.2
L	5	13.2	4	1.5	3	7.4	6	8.5	7	5.1	3	5.6
Original Number per section	12		6		6		6		6		6	

FIGURE 2. - Distribution of Anomala opacicollis larvae along Soil Moisture Gradients



% Moisture Content in the twelve trough sections.

TABLE 4. - Trials (ii) and (iii) from Table 3 combined, disregarding end sections.

Soil Moisture Content %	Number of Larvae
0.4	0.5 +
0.6	2
0.9	5
1.8	12
2.4	6
3.0	5
3.5	2
4.2	4
4.6	6
5.2	5
5.8	4
6.3	2
6.9	4

+ average of sections B to I inclusive, trial (ii).

To investigate the relationship between soil moisture content and the relative humidity of the soil air spaces, a number of 2 lb preserving jars were half filled with the same type of soil as used in the moisture content gradient experiments. This soil had been mixed with water to give various moisture contents, and "Edney" paper hygrometers were placed in the jars which were then sealed. It was found that 1.7% soil moisture content at room temperatures was the lowest that still gave 100% relative humidity of the air enclosed with the soil. Naturally, as the moisture content of the soil increases, so its air spaces are filled with water, and it is reasonable to suppose that the larvae prefer the soil moisture content which gives the maximum aeration of the soil while preventing desiccation by keeping the air spaces saturated.

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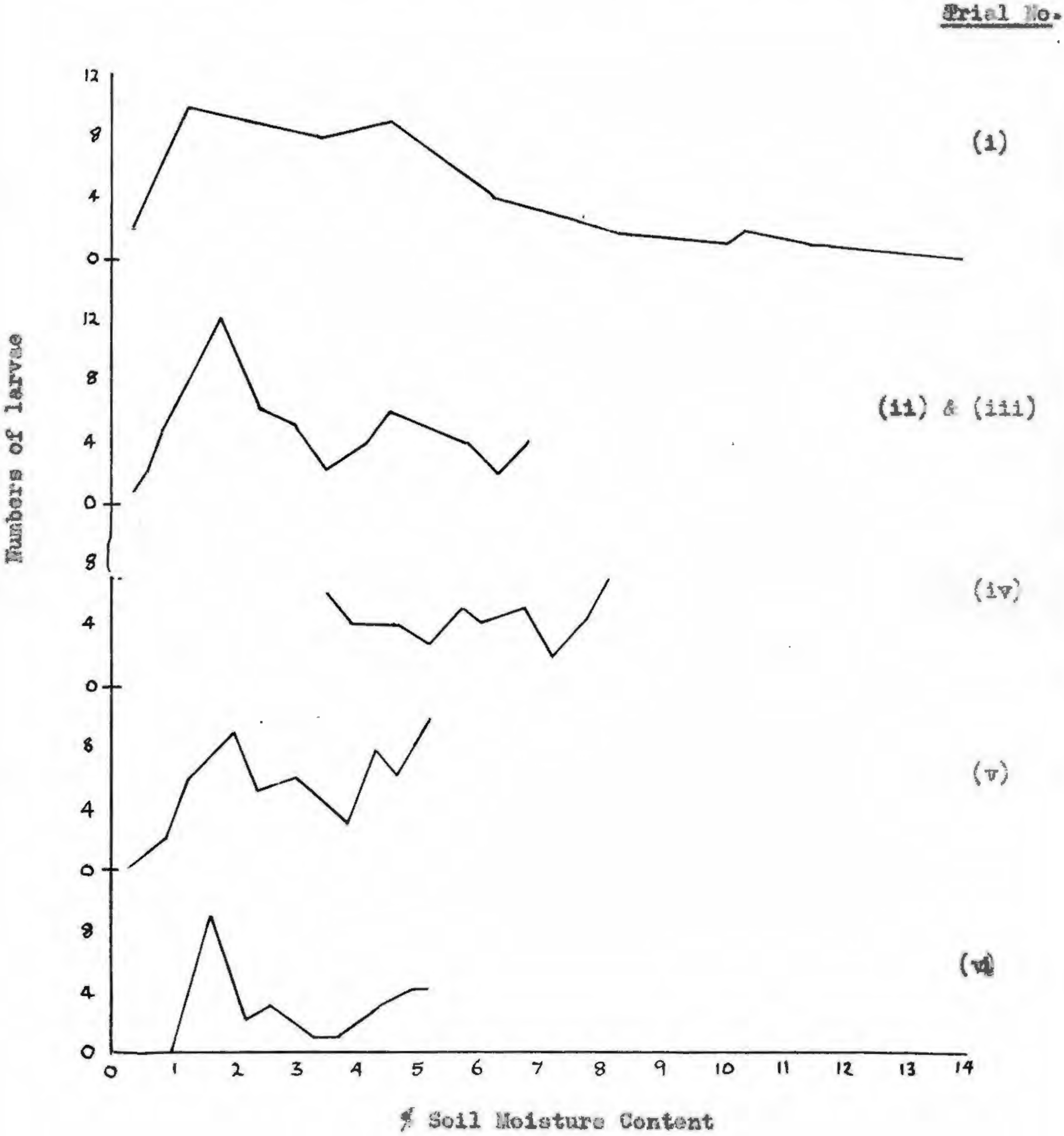
FIGURE 3. - **Distribution of A.opacicollis larvae along Soil Moisture Gradients**



In figures 2 and 3, it will be noted that anomalous concentrations of larvae tend to occur at trough ends. This phenomenon occurred in many of the gradient experiments and is useful in elucidating the mechanism of movement along step gradients. Discussion of this point will, however, be left until the end of the section on larval movements.

B. SOIL TEMPERATURE

For a proper estimation of soil insect movements along temperature gradients, apparatus which can keep a uniform temperature across the direction of the gradient is required. In the absence of such apparatus, an approximate estimate of relative preferences at different soil moisture contents was all that could be obtained. A steel trough was filled with soil of a uniform moisture content and was heated at one end with a spirit lamp and cooled at the other by a stream of water. Thermometers were introduced at 2 foot intervals along the trough through corked holes in the air-tight lid.

Once the temperatures were constant, larvae were introduced evenly along the trough, and, after one to two hours, the soil was removed in six inch vertical sections for larvae counts and soil moisture determinations. The thermometer bulbs were placed $1\frac{1}{2}$" above the bottom of the trough, and as most of the larvae were found below this level and hence in higher temperatures than those recorded, only relative preferences at the different soil moisture contents were obtained. Table 5 gives the results, and these are graphed in Figure 4. The temperature preferences at the different soil moisture contents are shown in Figure 5.

Reference/

Reference has already been made to the occurence of anomalous "end effects" in gradient experiments. However, the concentrations of larvae at the hot ends in the temperature experiments were due to a circumstance peculiar to these experiments. The heat was applied to the middle of the first section and, since heat would be lost from the end of the trough, the maximum temperature would occur some distance from the end of the trough. Any grubs caught in the first short gradient could not be expected to pass the maximum temperature into the main gradient to find the optimum temperature, hence a concentration at the hot end occurred.

The preference trend demonstrated in Figure 5 can be explained if the respiratory requirements of the larvae are considered. Desiccation must be avoided and thus a saturated atmosphere is a survival necessity. However, with increasing amounts of water in the soil, the air spaces are progressively filled until finally the aeration of the soil becomes less than that required by the larvae for respiration. Moreover, if the temperature is raised, the metabolic rate of the larvae becomes greater, and more soil aeration is required to satisfy the increased need for oxygen. Hence, as soil moisture content increases, the preferred temperature will decrease so that the metabolic rate is adjusted to the amount of oxygen available for respiration.

These results explain why chafer larvae can exist close to the soil surface near which the temperature is high and the soil moisture content relatively low.

Experiments/

TABLE 5. - <u>Distribution of Anomala opacicollis 3rd instar larvae along Temperature Gradients with different soil moisture contents.</u>

Distance along Gradient (inches)	Trial No.														
	i			ii			iii			iv			v		
	Larvae	Temp°F	MC.%	Larvae	Temp°F	MC.%	Larvae	Temp°F	MC.%	Larvae	Temp°F	MC.%	Larvae	Temp°F	MC.%
0 - 6	9			5			6			5			7		
6 - 12	0			0			0			0			0		
12 - 18	0	107.1	4.3	0	107.4	3.5	0	112.6	2.5	0	111.4	1.6	1	113.0	Air dried ≈ 0.5%
18 - 24	4	93.4		1	94.3		3	98.8		4	95.9		2	97.7	
24 - 30	5		4.4	15		3.7	8		2.3	12			11		
30 - 36	12	85.1		9	86.9		12	90.3		6	88.5		3	87.4	
36 - 42	9			7			12			8			6		
42 - 48	7	73.0	4.8	5	76.8	3.5	8	80.8	2.3	8	76.5	1.7	7	75.7	
48 -54	7			6			4			6			6		
54 - 60	5	70.7	4.5	4	72.7	4.0	4		2.6	9		1.9	4		
60 - 66	5			4			7			2			7		
66 - 72	3		4.5	3		3.4	4		2.3	4			3		
Average MC.			4.5			3.6			2.4			1.7			0.5
Mode		33.8"			28.4"			36.0"			27.6"			27.6"	

Original number of larvae per section = 6.

FIGURE 4. - Distribution of A.opacicollis larvae along Soil Temperature Gradients

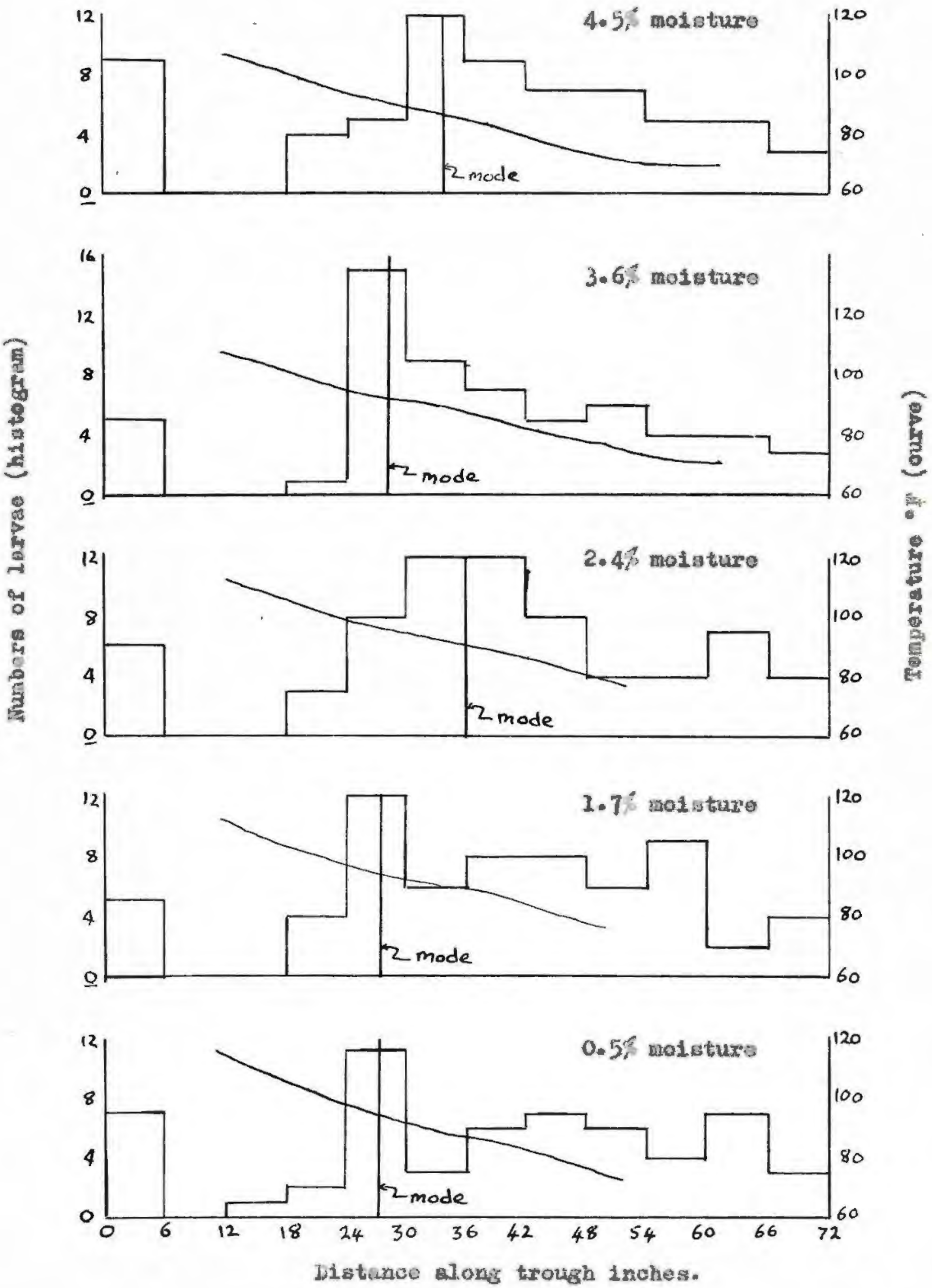


FIGURE 5. - Soil Temperature Optima of A.opacicollis larvae at Five Different Moisture Contents

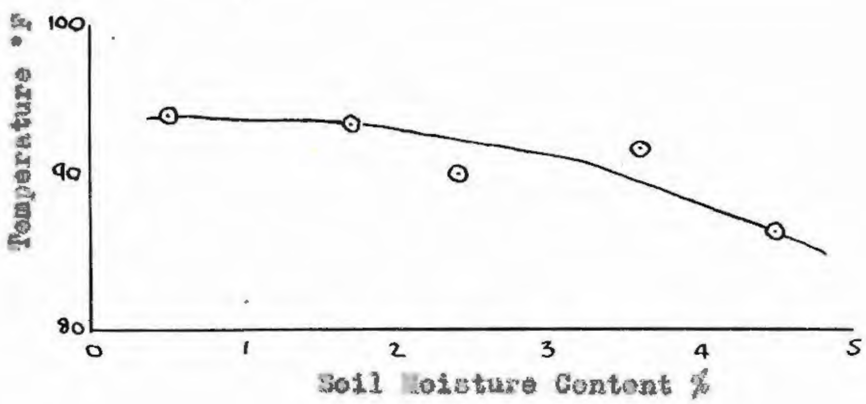
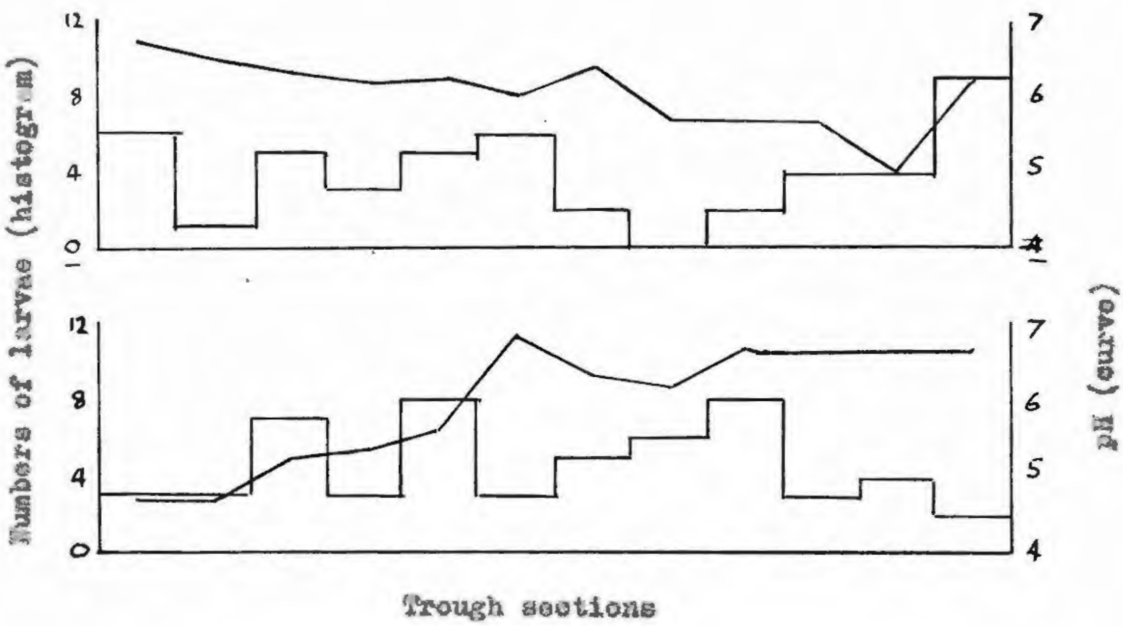


FIGURE 6. - Distribution of A.opacicollis larvae along soil pH Gradients



Experiments on the survival of larvae at different levels of temperature and soil moisture content will be described later, and these show that lethal temperature - soil moisture combinations are not likely to occur within the top 3" of soil where the larvae are active. In fact the high temperatures and low moisture contents that occur near the surface seem to be those preferred by the larvae.

C. pH

Soil samples were treated with 0.2% sulphuric acid and saturated lime water to give a range of pH values. Step-gradients were then set up in a trough and larvae introduced as described previously. The method was not successful in producing alkaline soil, but, in any case, this is not found within the sandveld areas. Table 6 gives the distribution of larvae after a week. The final pH values of the soil were obtained using a Beckman pH meter. Figure 6 shows that the distribution was erratic in the two experiments conducted and no preference was exhibited. The production of other pH differences in the soil produced other changes (eg. in calcium content); had preferences been found further separation of the factors involved would have been necessary.

D. SOIL COMPACTION

Sandveld soil with a uniform moisture content of 5% was packed into a trough to give a step-gradient of from 80 to 104 lbs soil per cubic foot. Table 7 and Figure 7 give the distribution of larvae a week after their introduction into the gradient. No preferences were demonstrated within the range of compaction tested. This range was adequate in relation to cultivated soils, although the upper limit was not as high as the compaction found in pathways or bare consolidated soil.

TABLE 6. - Distribution of Anomala opacicollis 3rd instar larvae along pH Gradients.

Trough Section	Trial No.			
	i		ii	
	Larvae	pH	Larvae	pH
A	6	6.7	3	4.7
B	1	6.5	3	4.7
C	5	6.4	7	5.2
D	3	6.2	3	5.3
E	5	6.3	8	5.6
F	6	6.0	3	6.8
G	2	6.4	5	6.3
H	0	5.7	6	6.2
I	2	5.7	8	6.7
J	4	5.7	3	6.7
K	4	5.0	4	6.7
L	9	6.2	2	6.7

Original number of larvae per section = 6

TABLE 7. - Distribution of Anomala opacicollis 3rd instar larvae along a soil compaction Gradient.

Trough Section	Larvae	lbs soil/ cubic foot
A	7	80
B	4	82
C	4	84
D	2	86
E	3	88
F	2	90
G	3	92
H	6	94
I	5	96
J	1	98
K	5	100
L	12	102

Original number of larvae per section = 6

E. FERTILISER

A fertiliser mixture (Virginia 'A') containing 6% N, 10% P_2O_5 and 8% K_2O was used to make a step gradient of fertiliser content in soil containing 5% moisture. The range was equivalent to applications from 0 to 1,000 lbs fertiliser per acre broadcast. Table 8 and Figure 8 show that no preference was demonstrated by the distribution of larvae one week after introduction into the gradient.

TABLE 8. - Distribution of Anomala opacicollis 3rd instar larvae in a Fertiliser Gradient.

Trough Section	Larvae	lbs fertiliser/ acre
A	11	0
B	3	92
C	2	185
D	7	277
E	3	369
F	6	461
G	3	554
H	3	646
I	7	738
J	4	831
K	6	923
L	10	1000

Original number of larvae per section = 6

F. COMPOST

Sand and kraal compost were mixed to make a step-gradient of compost content from 0 to 100%. Table 9 and Figure 9 show the distribution of larvae along the gradient one week after introduction. A definite preference for compost was demonstrated.

This/

FIGURE 7. - Distribution of A.opacicollis larvae along a Soil Compaction Gradient

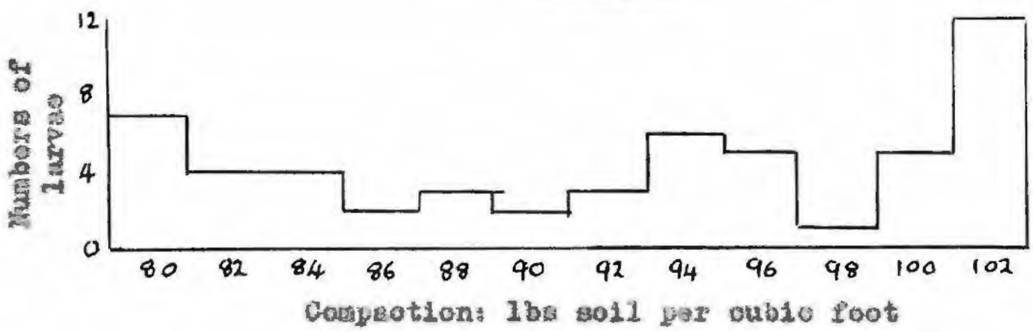


FIGURE 8. - Distribution of A.opacicollis larvae along a Gradient of Fertiliser Application

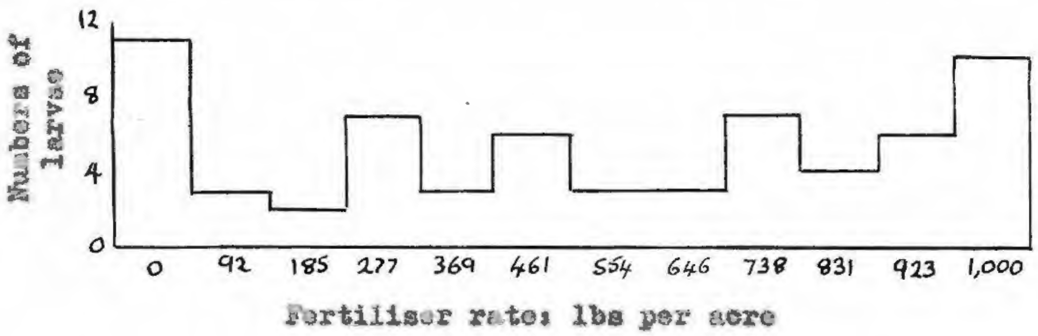
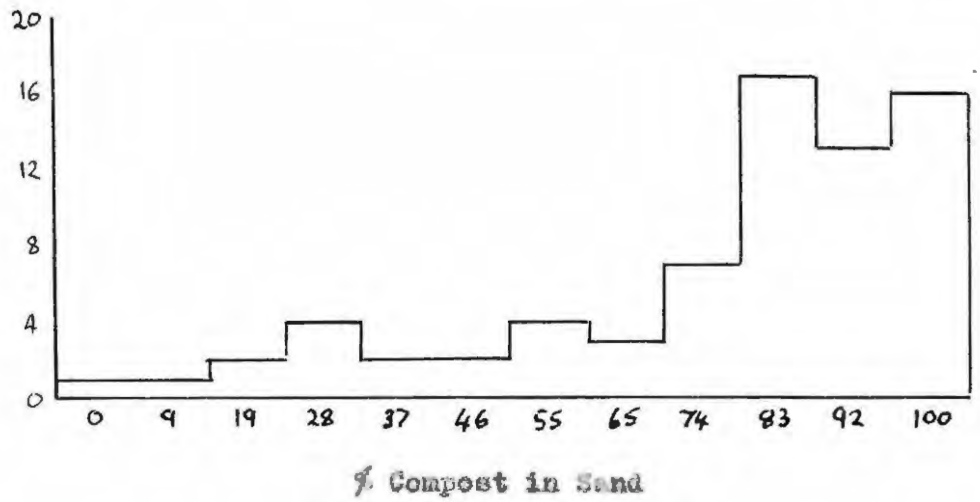


FIGURE 9. - Distribution of A.opacicollis larvae along a Gradient of Compost in Sand



This experiment indicates the reason for erratic distribution of larvae in the field. The larger particles of organic matter in the soil mainly originate from partly decomposed roots or leaves and will occur scattered throughout the soil as discrete concentrations of food material for the larvae. These, in turn, will tend to cause local concentrations of larvae.

TABLE 9. - Distribution of Anomala opacicollis 3rd instar larvae along a compost Gradient.

Trough Section	Larvae	% compost in sand
A	1	0
B	1	9
C	2	19
D	4	28
E	2	37
F	2	46
G	4	55
H	3	65
I	7	74
J	17	83
K	13	92
L	16	100

Original number of larvae per section = 6

G. PLANT DENSITY

Three troughs were filled with (i) sand, (ii) grey sandveld soil and (iii) kraal compost. Small tobacco seedlings were planted in these media to give gradients of seedling density. Larvae were introduced in the normal way and after two weeks, the troughs were emptied. Water was sprinkled evenly along the troughs as required throughout the experiment. Table 10 and Figure 10 give the distribution of the larvae

A slight preference for the high plant density appears to have been shown. However, the number of larvae in any section never exceeds the original number (c/f Tables 3,5 and 9). The root masses of the seedlings were small, and did not penetrate more than 1" into the soil whereas most of the larvae were found towards the bottoms of the troughs. No plants were attacked, although in the sand trough, there was no other food for the larvae. An absence of any marked chemotropic response to the plants is therefore apparent. Possibly the plant cover had some effect on the physical condition of the soil which enhanced the chance of survival of the larvae, although there was no direct evidence of this.

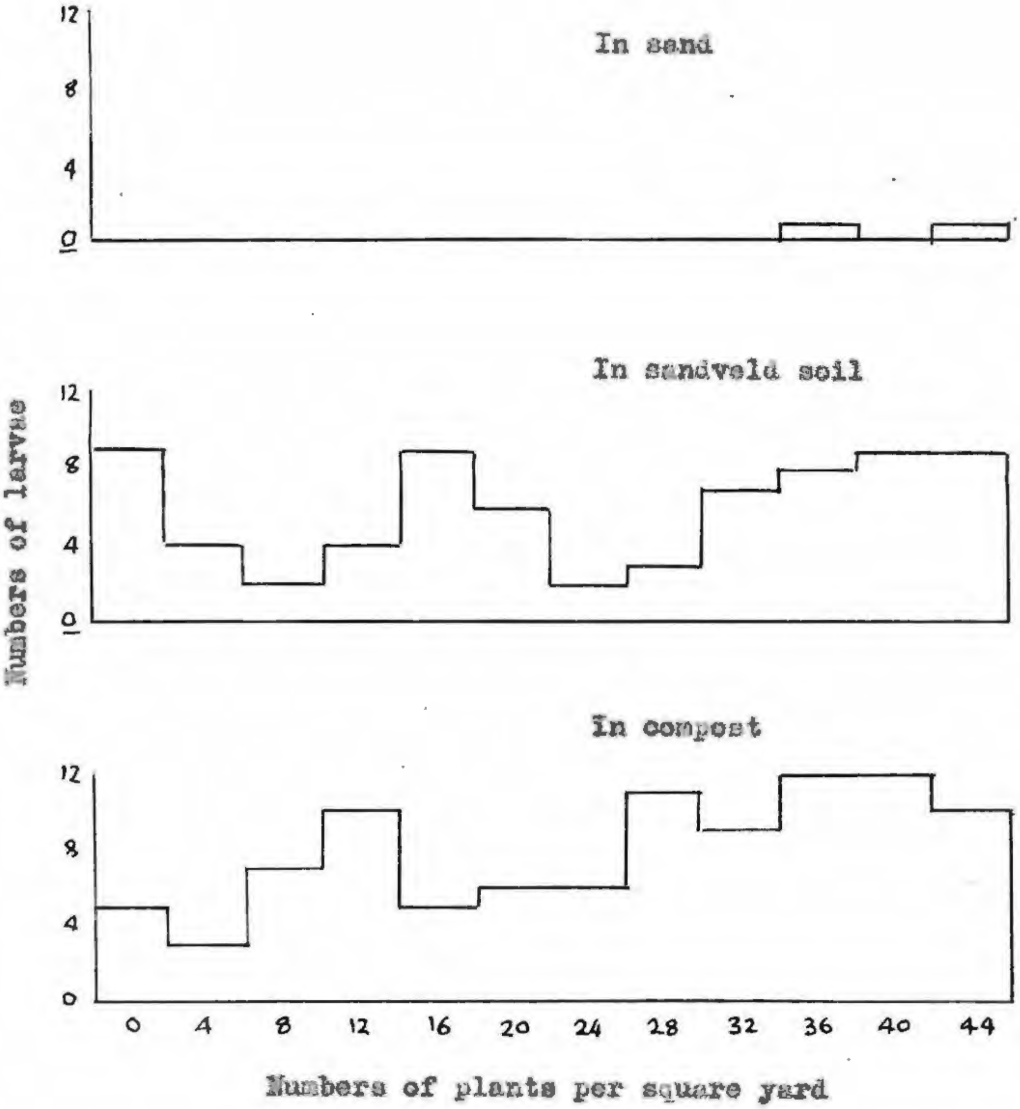
TABLE 10. - Distribution of *Anomala opacicollis* 3rd instar larvae along plant density Gradient.

Trough Section	Number of larvae			Plants/ yd²
	(i) in sand	(ii) in sandveld soil	(iii) in compost	
A	0	9	5	0
B	0	4	3	4
C	0	2	7	8
D	0	4	10	12
E	0	9	5	16
F	0	6	6	20
G	0	2	6	24
H	0	3	11	28
I	1	7	9	32
J	0	8	12	36
K	1	9	12	40
L	0	9	10	44

Original number of larvae per section = 12

H./

FIGURE 10. - Distribution of A. opacicollis larvae along Gradients of Tobacco Seedling Density



H. SOIL TYPE

Three soils, one an organic type (vlei soil), one a light sand (grey sandveld) and one a sandy loam (heavy red sandy loam), were placed in 6" vertical sections, one after the other, all the way along a 6 foot trough. Twelve larvae were introduced into every section and after a week their distribution determined. Table 11 shows that there was a definite preference for the typical sandveld soil and that the vlei soil was avoided. This result is in accordance with field observations on the distribution of whitegrubs.

TABLE 11. - Distribution of Anomala opacicollis 3rd instar larvae between three types of soil.

Numbers of larvae		
Organic	Light Sand	Sandy Loam
3	16	9
8	10	11
3	16	4
2	13	6
16	53	30

Original number of larvae per section = 12

3./

3. THE MECHANISM OF MOVEMENTS IN THE SOIL

The foregoing results must be interpreted with the realisation that, in most cases, the gradient was a step type and not true. The larvae were introduced into the middle of every step and they could not have sensed the adjacent steps before they moved into them. In the soil moisture experiments, it is conceivable that moisture may have diffused from wetter sections into dryer sections, tending to make a true gradient, but, in the compost experiment, it is difficult to see how any diffusion of organic matter particles could have occurred. Thus it is unlikely that the direction of these step-gradients directly influenced the direction of movement of the larvae. However the results can be explained if it is assumed that the speed of movement was affected by the gradient and that the further conditions departed from the optimum, the greater the speed of movement became. If such an assumption is correct, the probability of finding larvae in optimum conditions would have been greater than the probability of finding them in unsuitable conditions, and the distribution of larvae along the gradient would have varied accordingly.

One consequence of such a mechanism would be the occurence of anomalous concentrations of larvae at trough ends, the "end effects" which were, in fact, observed. These would arise in the following manner. If the direction of movement is unaffected, some larvae may move along the gradient in the wrong direction, but with increasing speed of movement, until finally stopped by the end of the trough. Of course, movement will generally be in random directions and there is no guarantee that once a larva has begun to move in one direction it will continue to do so, thus end concentrations will not be excessive.

To/

To put this theory to the test, larvae were marked with various paints so that the direction and extent of their movements could be gauged. Unfortunately the markings were soon lost once the larvae were in the soil and the results of this experiment were not conclusive. However, some confirmation of the theory was obtained. After one hour in a step-gradient of soil moisture content, sufficient markings remained to show that the larvae had moved in both directions along the gradient and that, as a result, concentrations at the ends of the trough and at the optimum moisture content in the middle of the trough were beginning.

With regard to "end effects" in other experiments none were found at the "dry" ends in the moisture gradients (Figure 2). However, only living larvae were recorded in these experiments and, since conditions dryer than the optimum were lethal, any larvae that did become concentrated at the "dry" ends would have died and would not have been recorded. Atfirst, it was thought that the concentrations at the "wet" ends were due to inability of the larvae to move once in soil of high moisture content. However, this could not have been the case since end-of-gradient moisture contents in some trials were repeated in the middle of gradients in others. No "end effects" were recorded in the compost gradient. Here the one end (pure sand) was lethal to the larvae (see Table 10) and any end effect at the compost end would have been marked, since the optimum was at or close to this end. Finally, "end effects" were also observed in experiments that gave negative results. The ordinary sandveld used in these experiments contained little organic matter and the general speed of movement must have been fast, resulting in the end concentrations. On the other hand, the "plant density" in compost" experiment/

experiment, in which the general movement must have been slower, did not result in an "end effect".

Under natural field conditions, the temperature and soil moisture gradients will be true gradients and may well affect the orientation of larval movement. However they will mainly be vertical gradients and will not affect the horizontal distribution of larvae to any great extent. It appears, in fact, that organic matter in the soil will be the main factor determining distribution, and organic matter content of the soil does not vary in a regular manner. Thus discrete concentrations of organic matter will give rise to discrete concentrations of larvae and this would account for the local variations in land population found. If the theory of movement outlined above is correct and the general level of organic matter in a soil is low, the movements of any larvae present will be correspondingly fast and this may affect the amount of damage inflicted by the larvae on field crops. Thus if tobacco is planted in soil generally poor in decaying organic matter, whitegrubs will move about more and be more likely to find and attack the plants than if the tobacco had been planted in a richer soil. Such does appear to be the case and a further reference will be made to this point in the section on ploughing in relation to chafer larvae.

4./

4. THE SURVIVAL OF LARVAE IN RELATION TO SOIL TEMPERATURE AND MOISTURE CONTENT

Chafer larvae die from desiccation unless they are kept in a saturated atmosphere. They also die if kept in sealed containers, presumably through asphyxiation. Thus soil in which they are kept for observation must be kept moist and well ventilated. In the absence of suitable apparatus, it was not possible to maintain a constant moisture content in soil samples over long periods, so the effect of soil moisture content and temperature on the rate of larval development could not be measured. However, the effect of these factors on survival over short periods was measured in the following manner. An incubator was set at a required temperature and provided with large trays of water to keep the air inside as nearly saturated as possible. Batches of larvae were placed in a soil-compost mixture of desired moisture content in containers and these were placed unsealed in the incubator. Using this method, a series of soil moisture contents were tested at 98 °F, and a series of temperatures were tested at an initial soil moisture content of 5%. Tables 12, 13 and 14 give the results obtained and the data from Tables 13 and 14 is graphed in Figures 11 and 12.

The optimum moisture content of the soil-compost mixture used appears to be between 10 and 40%, and this is much higher than the optimum for the sandveld soil used in the gradient experiments as measured by larval preferences. However, the saturation point for the sandveld soil was 15% moisture content, whereas with the soil-compost mixture it is 70% It has already been suggested that optimum moisture contents depend on the aeration of the soil and the relative humidities of the air spaces rather than the absolute amount of moisture present.

Thus/

Thus the high optimum for the soil-compost mixture probably reflects the greater aeration and moisture capacity of the soil when compost is added.

TABLE 12. - Mortalities in batches of 3 Anomala opacicollis 3rd instar larvae in a Soil-compost mixture at 98°F.

Soil Moisture Content %	Hours 20	25	50	66
1.5	3			
3.5	1	3		
4.0	0	3		
4.5	3			
5.0	0	1	3	
5.5	1	1	3	
6.0	1	3		
7.0	1	2	3	
9.0	0	0	2	3
10.0	0	1	2	2
15.0	1	3		
20.0	0	1	2	2
30.0	0	3		
40.0	0	0	1	2
50.0	0	1	3	
60.0	0	1	3	
70.0 +	0	3		
80.0 +	0	3		

+ saturated

TABLE 13. - Mortalities in batches of 12 Anomala opacicollis 3rd instar within 24 hours after exposure to temperatures for periods up to 4 hours.

Temp. °F	Batch	Hours exposure 1	2	3	4
65 - 75 (Room)	1	1	1	1	0
	2	0	2	1	1
	3	0	2	2	2
	Total	1	5	4	3
95	1	2	1	1	0
	2	0	2	1	0
	3	2	0	0	1
	Total	4	3	2	1
99	1	1	2	2	3
	2	2	2	2	0
	3	1	1	1	2
	Total	4	5	5	5
104	1	1	4	2	2
	2	1	2	4	1
	3	0	2	1	3
	Total	2	8	7	6
108	1	0	0	12	12
	2	0	0	11	12
	3	0	1	11	12
	Total	0	1	34	36
113	1	0	11	12	12
	2	0	7	12	12
	3	0	12	12	12
	Total	0	30	36	36
116	1	12	12	12	12
	2	12	12	12	12
	3	12	12	12	12
	Total	36	36	36	36

The temperature data indicates that temperatures as high as 104 °F can be withstood for a period of four hours, but that prolonged exposure to 101 °F is normally lethal.

TABLE 14. - Mortalities in batches of 12 Anomala opacicollis 3rd instar larvae after 5 days at constant temperatures.

Batch	Temperature °F					
	65-75	95	97.5	98.5	101	102
1	0	2	0	2	7	11
2	0	3	1	0	8	12
3	1	2	1	3	4	9
4	4	2	0	1	7	10
5	0	5	1	0	7	10
6	1	0	2	2	12	11
Total	6	14	5	8	45	63

The curve in Figure 12 shows an anomalous peak at 95 °F, but Table 14 shows that this was not due to any freak observations, as the data for the different batches is consistent. A possible explanation is that a disease organism attacking the larvae was particularly active at this temperature. It was noticed that many of the larvae used in the experiment developed black patches in the epidermis and these were later recognised as symptoms of a virus disease. Apart from the temperature differences, all the batches of larvae were treated in the same way and it is conceivable that the virus was most active at 95 °F.

It is interesting to consider the temperature data in relation to normal soil temperatures at Trelawney. At 2" below soil surface, the temperature may rise above 100 °F at midday, but at 4" it is seldom above 95 °F.

Moreover/

FIGURE 11. - <u>Total Mortality in 3 batches of twelve A.opacicollis larvae within 24 hours of Short Exposures to high Temperatures</u>

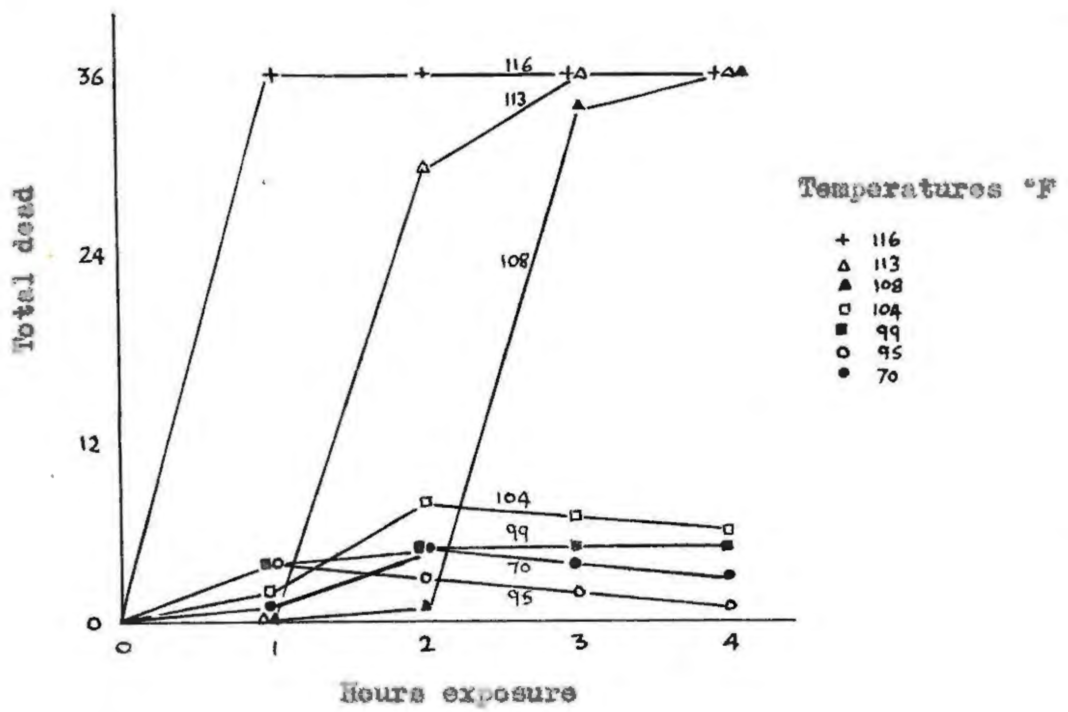
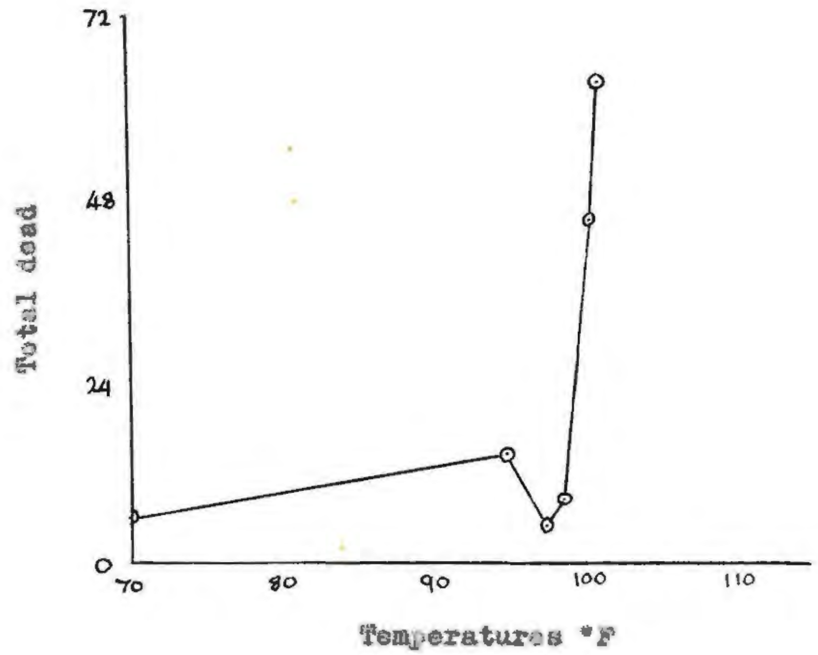


FIGURE 12. - <u>Total Mortality in 6 batches of twelve A.opacicollis larvae after continuous exposure to various Temperatures for 5 days</u>



Moreover the high temperatures are seldom maintained for more than 4 hours. It appears, then, that temperature alone will not be a limiting factor in the survival of the larvae in the soil. The optimum temperature for survival in these tests appears to be in the region of 97 °F, while in the gradient experiments, a rough estimate of the preferred temperature at the lowest moisture content giving saturated air spaces was 94 °F and it was known that this estimate tended to be too low. It is likely, therefore, that larvae are attracted to the top 3" of soil since it is here that the optimum conditions of temperature and moisture are most likely to exist.

5./

5. THE MOVEMENTS OF PREPUPAE

Prepupae have been found at greater depths in the soil than the active larvae. An experiment was conducted to determine whether there is a general downward trend of movement of prepupae and, if so, whether this is influenced by soil moisture.

Porous concrete pipes of 4" internal diameter were placed in 12" diameter metal cylinders sunk vertically into the ground. The cylinders were filled with water to produce a water table and the level of the water was kept constant. The concrete pipes were filled to within 9" of ground level with sand and the remaining portions with sandveld soil. Four prepupae were introduced into every pipe in early April and the pipes were emptied a week later when the positions of the grubs and the vertical soil moisture content gradients were determined. Tables 15 and 16 summarise the results of the experiment and Figure 13 gives the graphs of the soil moisture content gradients.

TABLE 15. - % Soil moisture contents in six vertical gradients.

Depth in	Pipe No.					
inches	1	2	3	4	5	6
0	18.5	11.8	6.4	2.9	0.8	0.5
6	28.8++	17.6	10.4	6.7	5.0	3.7
12		24.0+	24.1+	11.1	7.9	6.3
18			24.0+	24.3+	11.2	8.8
24				24.1+	24.4+	13.2
30					24.0+	24.3+
36						24.5+

\+ saturated

++ the top 9" of soil had a higher moisture capacity than the sand beneath.

TABLE/

TABLE 16. - Depths of *Anomala opacicollis* prepupae in the six moisture Gradients recorded in Table 15.

Prepupa No.	Pipe No.					
	1	2	3	4	5	6
1	1"	6"	8"	7"	6"	7"
2	4"	9"	1"	14"	14"	13"
3	6"	9"	9"	3"	11"	13"
4	5"	8"	12"	8"	8"	23"
Mean	5"	8"	7.5"	8"	10"	14"
% M.C. at Mean +	++	+++	12	8	7	7

\+ estimated from Figure 13
++ saturated
+++ near saturation

It is apparent from these results that prepupae do move below the topsoil in which the active larvae are found. Saturated soil impeded this movement in the experiment, although the prepupae did descend into moisture contents far higher than are found in the veld at comparable depths. However, since the temperatures are low at these depths and activity is at a minimum, the prepupae presumably do not require well aerated soil.

FIGURE 13. - Soil Moisture Gradients in six Vertical Pipes used to observe movement of A.opacicollis prepupae(see Tables 16 & 15)

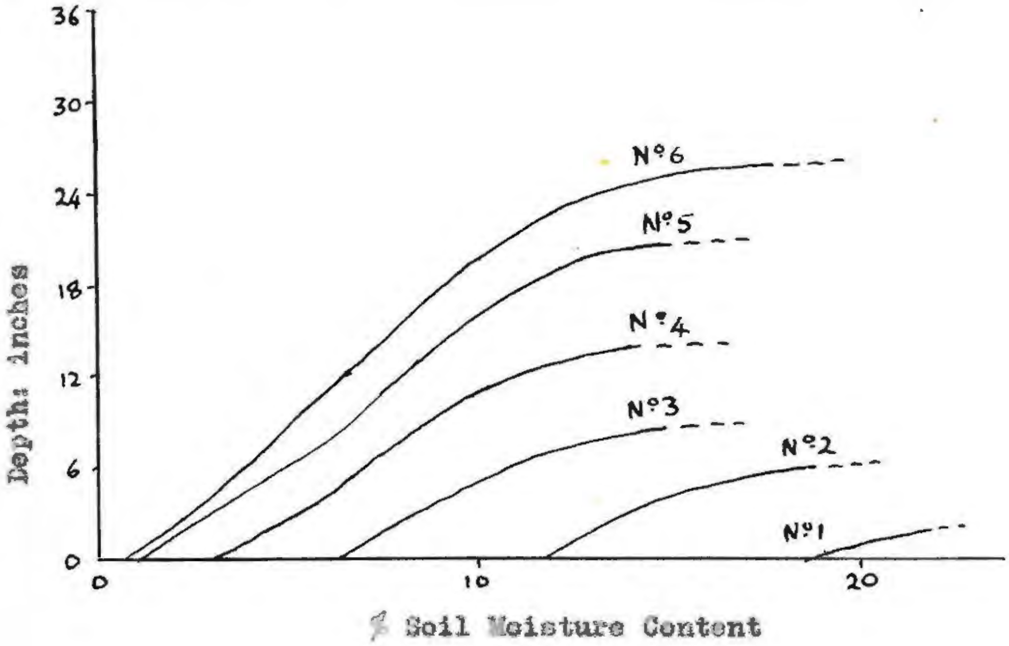
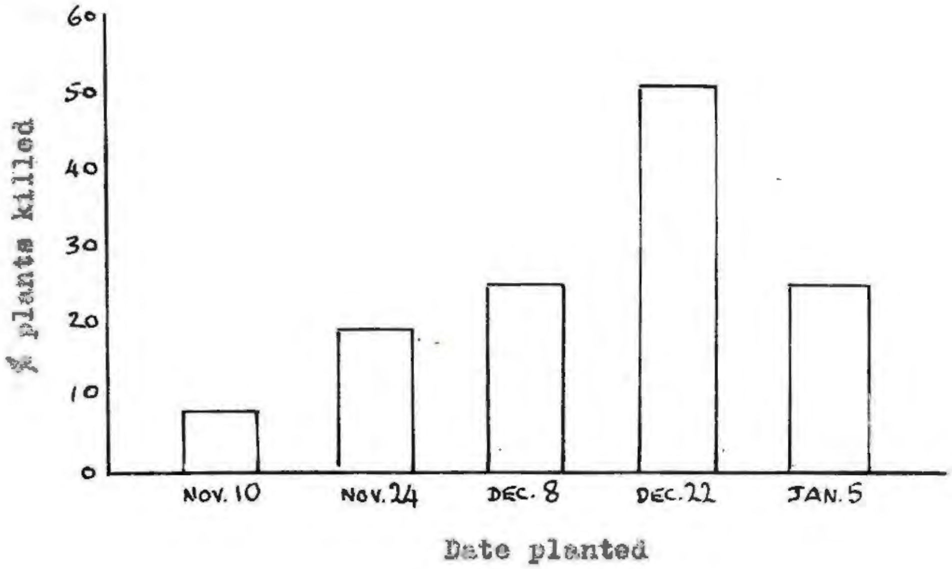


FIGURE 14. - Whitegrub damage to tobacco planted at five different dates in a heavily infested land



V. THE BEHAVIOUR OF WHITEGRUBS IN RELATION TO TOBACCO CULTURE

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Although the behaviour of only Anomala opacicollis has been considered above, much of the information would apply equally well to other Anomala species, and some of it to Schyzonycha and Adoretus spp. Together, these three families comprise practically all the whitegrubs found in the Southern Rhodesian sandveld, and experiments have indicated that all show similar reactions to soil temperature, moisture content and organic matter content. Moreover field observations suggest that all the adults exhibit much the same behaviour with regard to egg-laying. Thus the following account of the behaviour of whitegrubs in relation to tobacco culture, although primarily based on experiments with A.opacicollis, applies equally well to all Rhodesian whitegrub species.

1./

1. THE EFFECT OF PLOUGHING ON LARVAL DISTRIBUTION

The effect of ploughing on chafer larvae (whitegrubs) was first investigated in Southern Rhodesia by Mitchell (1946 b) and later by Moffett (1947). In their experiments, the numbers of whitegrubs and the numbers of tobacco plants damaged by whitegrubs respectively were recorded in plots of virgin soil ploughed either before the chafer beetle flight period or after the flight period. Their results are summarised in Tables 17 and 18 and show a preponderance of whitegrubs in the early ploughed plots.

TABLE 17. - Numbers of whitegrubs (all species) in early and late ploughed Virgin Plots.

Time of ploughing	Number of grubs in 140 square yard samples at the end of January, 1946
May, 1945	1,289
19th-20th November, 1945	909

Adapted from Mitchell (1946 b)

TABLE 18. - Plant losses due to whitegrubs in early ploughed Virgin and Second Year Plots and late ploughed Virgin Plots

Land Type	Ploughing Time	Total Stand losses due to whitegrubs
2nd yr.	May, 1946	273
Virgin	March, 1946	352
Virgin	15 November, 1946	210

Adapted from Moffett(1947)

Mitchell/

Mitchell found that Anomala spp. predominated in the whitegrub populations he recorded but, with reference to Table 2 of this thesis, it appears that Anomala spp. are more likely to lay eggs in the veld than in ploughed land. In other words, when the behaviour of the adults is considered, the late ploughed plots would be expected to contain more grubs. Although these results appear to be contradictory, they can be reconciled in the following way.

(1) With reference to Figure 1, it appears that there is a concentration of whitegrubs at the edge of the land. This land was ploughed early, before the chafer beetle flight period, and if the beetles laid their eggs in the veld in preference to the ploughed land, those portions of the land adjacent to the veld would be expected to have the heaviest infestations.

(2) This evidence was corroborated by three lines of pest samples taken in another early ploughed land. Table 19 shows that, again, whitegrubs were concentrated at the edge of the land. Moreover it appeared from these samples, and from the distribution map in Figure 1, that, as a rough estimate, the "border effect" extends for some 50 to 60 feet into the land.

TABLE 19. - Whitegrubs in 40 two-foot samples of ridge at the edge and next to the edge of an early-ploughed tobacco land

Line No.	Within 60 foot of edge	Next 60 foot
1	63	16
2	40	17
3	14	0

(3)/

(3) It is now possible to explain Mitchell's and Moffett's results in terms of a "border effect". The plot size used in these experiments was 46 yards by 11 yards. Mitchell had his treatments (ploughed early and ploughed late) replicated seven times, giving a total of 14 plots. These were divided into 2 blocks, one of 8 plots on "loose sandy soil" and the other of 6 on "heavy sandy loam". However these plots were arranged, in neither block would any one plot be free from a 60 foot "border effect". In any case there would be a "border effect" around every late plot and this would interfere with adjacent early ploughed plots. A similar argument can be put forward with regard to Moffett's results.

(4) Point (3) explains the presence of whitegrubs in early ploughed plots, but not their numerical superiority. However, the direct effect of late ploughing on the grubs already present must be taken into account. Whitegrubs live in the top 6 inches of soil during their active period and, since they are soft bodied creatures, they would be liable to mechanical injury. Moreover, ploughing would expose them to natural enemies. Birds can often be seen searching through ploughed lands for insects, while carnivorous beetles and ants are known to attack exposed whitegrubs. Thus, it can be assumed that, due to a "border effect", both ploughed and unploughed virgin plots in Mitchell's and Moffett's experiments were infested with comparable numbers of grubs by mid-November and that, due to the late ploughing, there was some reduction in the plots so treated.

(5) In the oviposition experiment (Table 2), there was no border effect, but the plots were isolated, one from another, by concrete partitions. The/

The inference that can be drawn is that the border effects in early ploughed lands are due to the diffusion of whitegrubs from the unploughed border. There is no gradient from unploughed to ploughed land and the theory developed on movements in step gradients suggests that any whitegrubs in the unploughed veld and near to the ploughed land may well cross over. If the land has been ploughed long enough for most of the original vegetation to have rotted down and disappeared, these grubs would have to move considerably to obtain all the food material they require, and thus a region of the ploughed land adjacent to the unploughed veld will become populated.

In a moisture gradient experiment in which the larvae were marked with paint, some of these were found to have travelled towards the optimum through more than one foot of soil in one hour. Hence it would be possible for whitegrubs to travel some 60 feet into a ploughed land within two or three months.

To summarise, although early ploughed land may have whitegrub infestations in a 60 foot border round the land, late ploughed virgin land may have an infestation throughout the whole land. With second or third year land, the infestation will depend on the amount of vegetation present during the beetle's flight period. If the soil is hard and bare, it may be even less attractive to egglaying females than if it is ploughed (Table 2), but with a heavy weed cover, the position will be much the same as with virgin land.

2. SOIL FERTILITY AND LARVAL ACTIVITY

The amount of organic matter present in the soil determines both its attractiveness to egg-laying chafer beetles and the activity of any whitegrubs in it. If manure is spread on a land before November, the beetles will be attracted to it and it will be more likely to contain whitegrubs. At the same time it has been suggested that whitegrubs do not move as fast in soils with a high content of organic matter. However the first influence overshadows the second since it is a matter of common observation that the chance of whitegrub damage to tobacco plants is increased by manuring. Certainly the cattle kraal land, for which the whitegrub distribution is mapped in Figure 1, contained many more whitegrubs than adjacent normal lands and the tobacco in it was more heavily attacked in consequence.

Second and third year tobacco lands contain less organic matter than first year (virgin) lands. However, with early ploughing, it appears that few beetles will be attracted to lay eggs in a land whether it is in the first, second or third year of cultivation. Most of the whitegrubs which occur in it will have moved in from the surrounding veld, and their numbers will not be greatly influenced by the age of the land. However, the soil in second and third year lands will be poorer in organic matter than in first year lands and it is suggested that any whitegrubs present will tend to move about more. If this is the case the tobacco will be more likely to be found and attacked. This would explain the contention of many tobacco growers that second and third year land is more heavily infested with whitegrubs than first year land. Actually the infestations may be just the same, but the activity greater in the former.

3. TIME OF PLANTING IN RELATION TO WHITEGRUB DAMAGE

It has already been noted that whitegrubs reach the third instar, and begin to damage tobacco seriously, by the end of December. Data on the relative damage done to tobacco planted at five different dates (page 41) in a heavily infested land is given in Table 20 and Figure 14. The drop in damage in the last planting was due to the cessation of feeding by some of the larvae which had begun to turn into the prepupal stage. Advantage cannot be taken of this drop as growing conditions are unsuitable for tobacco planted this late. However tobacco planted at the beginning of November normally yields much more and is of better quality than tobacco planted in late December and simultaneously it will suffer less than one fifth of the soil insect damage.

TABLE. 20 - Plant losses caused by whitegrubs in Five tobacco plantings.

Date of planting	Plant losses
10th November	8%
24th November	19%
8th December	25%
22nd December	51%
5th January	25%

VI. THE/

VI. THE BEHAVIOUR OF WHITEGRUBS IN RELATION TO INSECTICIDES

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1. THE REPELLANT ACTION OF SOME INSECTICIDES

To determine the relative effectiveness of a number of insecticides in controlling A. opacicollis larvae, larvae were placed in batches in 1 lb preserving jars containing soil mixed with the insecticides. It was found that within the confines of the jars, even small concentrations of insecticides caused total mortality, although the rates of insecticidal action depended on the concetration. However, in all jars in which the soil had been treated, a certain number of larvae came to the surface of the soil, whereas in the control pots all remained within the soil. Moreover the numbers found on the surface differed with the different insecticides, showing that some of these had a greater repellant action than others. Table 21 summarises these results.

TABLE 21. - Per cent Anomala opacicollis larvae repelled by concentrations of insecticides giving comparable mortality rates in an enclosed space.

Insecticide	% Repelled
Chlordane Emulsion	50
Parathion Suspension	25
B.H.C. Suspension	21
Toxaphene Dust	71
D.D.T. Suspension	62
Control	0

2./

2. WHITEGRUB DISTRIBUTION IN RELATION TO FIELD TRIALS

The erratic distribution of whitegrubs in the soil causes certain difficulties in making accurate estimates of the effectiveness of insecticide - treatments in the field. Straight counts of the numbersof pests present in soil samples, or the numbers of plants attacked gives little indication of the effectiveness of the treatment: all that is obtained is an indication of the number of survivors from an unknown original population which might have been big or small.

One method of treatment assessment is to sample the population in every plot before and after treatment (Mitchell 1946 b). However insecticides are normally applied around each individual plant and where an insecticide has a marked repellant action it may protect the plants without killing many larvae. Moreover it is possible that some insecticides inactivate larvae for some considerable time before they die (Moffett, 1947) and it is not always easy to distinguish between an inactive and an active whitegrub.

It appears essential, then, to lay out a control plot by the side of every treated plot and to compare the two. If small plots are used and it can be assumed that the initial insect activity is the same in adjacent treated and untreated plots, then a measure of initial activity is obtained and hence of the drop in activity associated with the treatment. This method of treatment assessment has been discussed elsewhere by the writer (Miles, 1953) and has proved successful where other methods have failed due to the erratic whitegrub distribution.

VII. SUMMARY

VII. SUMMARY

The larvae of Anomala opacicollis (Fer), of Melolonthid and of other Rutelid species, attack tobacco in Southern Rhodesia, and are more commonly called "whitegrubs". Whitegrubs are widespread in the sandveld areas where tobacco is grown and, at the Trelawney Station of the Tobacco Research Board of Southern Rhodesia, where this work was done, A. opacicollis was the predominant species.

An account of the one year life cycle is given.

The adults eat the leaves of various indigenous trees and an account of an experiment on the food preferences of A.opacicollis adults is given, and the main food sources in the Trelawney area are listed.

An experiment is described which shows that the beetles prefer to lay their eggs in the veld or in manured broken land rather than in normal ploughed lands.

The larvae are erratically distributed in lands and experiments on larval movement suggest that this is mainly due to concentration of the larvae at discrete concentrations of organic matter in the soil. The temperature and moisture conditions of the top 3" of soil are found to be those which attract the larvae. It is suggested that the larvae prefer and move to soil which contains the lowest amount of moisture which keeps the soil air spaces saturated. It appears that the preferred temperature decreases with increasing soil moisture content and it is suggested that this is due to the respiratory requirements of the larvae.

Soil pH, compaction and fertiliser content and the presence of plants do not appear to influence larval movements.

A/

A theory is developed concerning the mechanism of movements in the soil and it is suggested that, in the absence of a continuous gradient, the speed but not the direction of movement is influenced by conditions to which the larvae are sensitive. Evidence in support of this theory is given.

Studies on the survival of larvae at different soil moisture contents and temperatures show that conditions in the top 3" of soil are not likely to be lethal in spite of the high temperatures and low moisture contents found there.

The relation of whitegrub behaviour to agricultural problems is discussed. Other workers published evidence indicating that early ploughed lands were attractive to whitegrubs; this is shown not to be the case and the previous evidence is re-interpreted. Such lands tend to contain concentrations of whitegrubs round the borders. The reason for this is discussed and it is suggested that lands should be ploughed early to confine whitegrub infestations in this manner. Soils low in fertility through repeated cultivation are commonly believed to contain more whitegrubs than virgin soil. However, behaviour studies suggest that it is the activity and not the size of the population which is affected by soil fertility.

The time at which tobacco is planted is known to determine the extent of subsequent whitegrub damage. The reason for this is to be found in the life cycle of whitegrubs and the results of an experiment on time of planting in relation to whitegrub damage are given.

Some/

Some insecticides are shown to be more repellant than others to A.opacicollis larvae and the influence of this fact on the assessment of soil insecticide effectiveness in the field is discussed. Reference is made to a method developed by the writer for the determination of insecticide effectiveness under the conditions of erratic whitegrub distribution which normally occur.

VIII. REFERENCES

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