

THE VERTICAL DISTRIBUTION OF THE ROOT-KNOT NEMATODE (*MELOIDOGYNE JAVANICA*)  
IN A RHODESIAN SANDY SOIL<sup>1</sup>

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SUMMARY

Weekly changes in the vertical distribution of root-knot nematodes in the soil were measured under three cropping systems consisting of three years of *Tagetes minuta* or *Eragrostis curvula* var. Ermelo followed by tobacco (*Nicotiana tabacum* var. Kutsaga 51) and four years of tobacco. Soil samples were taken to a depth of five feet over a period of 19 months and bioassayed with tomato plants.

The largest numbers of root-knot nematodes were found under continuous tobacco, the smallest under *E. curvula* and intermediate numbers under *T. minuta*. The nematodes were found to depths of at least five feet but occurred mainly in the upper 30 inches of soil. Few were found in the hot, dry top three inches of soil, and the significance of this is discussed in relation to cultural and control practices currently used in tobacco production in Rhodesia.

INTRODUCTION

Despite the importance of the root-knot nematode, *Meloidogyne javanica* (Treub), in the production of tobacco in Rhodesia, comparatively little is known of its general ecology and the changes in its population density caused by physical factors and cultural practices under local conditions.

The vertical distribution of root-knot nematodes in Rhodesia has been studied by Daulton (1951) and Jack (1944), the former finding none below a depth of 25 in in a sandy soil with a heavy clay subsoil at about 18 in, while the latter only sampled the top 6 in of soil and found that the population was depleted in the top 4 in during the late winter and early summer. Rostron (personal communication) has found root-knot galls on tobacco roots at depths of 5 ft in root growth experiments at Kutsaga.

Of the plants used in the rotations, *T. minuta* showed nematicidal effects in greenhouse trials (Daulton and Curtis, 1963), and *E. curvula* var. Ermelo is recommended for rotation with tobacco in Rhodesia, since it

is resistant to *M. javanica* (Daulton, 1964). This paper reports the vertical distribution of *M. javanica* in a sandy soil under a rotation experiment from August, 1965, to March, 1967.

METHODS AND MATERIALS

FIELD STUDIES

The experimental site was at Kutsaga Research Station, near Salisbury.

The rotations were three years of *Tagetes minuta* L. followed by tobacco; three years of *Eragrostis curvula* (Schrad). Nees var. Ermelo followed by tobacco; and tobacco (*Nicotiana tabacum* L. var. Kutsaga 51) planted yearly for four years (continuous tobacco). Sampling commenced in August, 1965, prior to the third year of the rotation.

Samples were taken at 3 in increments down to a depth of 5 ft from the treatment plots at weekly intervals using a soil auger of 3 in internal diameter. All depths were measured from the soil surface except under tobacco, where they were measured from the top of the ridge. The top inch of each sample in the auger was discarded and the auger cleaned between samples to avoid contamination. Replicated samples from the same depth and treatment were bulked and mixed in a Tyler soil sample splitter.

Each combined sample was placed in a 6 in x 10 in polythene bag, filling it to a depth of 6 in (approx. 1,600–1,700 g soil). Holes were punched in the bottoms of the bags, which were stacked in the greenhouse at 75°F–95°F on asbestos slats over a corrugated bench to allow adequate drainage. The top inch of each bag was folded down, to make it more rigid and to provide a 3 in high splash guard above the soil to prevent contamination. Asbestos sheets 8 in high were placed around each set of samples to shade the sides of the bags and to prevent contamination.

A three-week-old nematode-free tomato seedling (*Lycopersicon esculentum* Mill. var. Rutgers), propagated in steam-sterilized soil

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in 2 in pots, was planted in each polythene bag. The samples were carefully watered three times daily by a fine spray which did not cause splashing. Twice a week each sample was given 50 ml of 1:1,000 Welgro liquid manure (15 per cent. nitrogen, 30 per cent. soluble phosphoric acid, 15 per cent. potash, plus trace elements). The tomato plants were grown for six weeks and their roots were then assessed for galling (Daulton and Nusbaum, 1961).

Soil moisture was measured by the weight lost on heating to 105°C for 24 h from samples taken at weekly intervals at depths of 0-3, 9-12, 21-24, 45-48 and 57-60 in in the rotations. Soil temperatures were recorded at 8 a.m. and 2 p.m. daily at depths of 2, 4 and 8 in. Rainfall for the previous 24 h was measured on the experimental site at 8 a.m. daily.

#### LABORATORY STUDIES

The effect of soil moisture on the survival of *M. javanica* was studied by comparing the nematode population levels in air-drying soil with those in soil kept moist (Koen, 1966). Population counts were made at the start and at weekly intervals; living *M. javanica* larvae were extracted from two 200 g soil samples from each treatment by a modified Seinhorst's two Erhlenmeyer flask method (Seinhorst, 1956). At the same time three soil samples from each treatment were planted with tomatoes for bioassay of *M. javanica* eggs and larvae. Soil moisture in each treatment was determined at each sampling.

The effect of soil temperature on *M. javanica* populations in the soil was investigated by heating soil samples to temperatures between 95°F and 120°F at 5° intervals for periods of 10 min. In one trial the soil was allowed to dry out during heating and in another it was kept moist. Three extractions and two bioassays were carried out on each treatment.

#### RESULTS

##### *Tagetes minuta*/TOBACCO ROTATION

Towards the end of the *T. minuta* crop during January, February and March, 1966, the *M. javanica* population increased substantially—particularly in the upper 27 in of soil but also down to at least 5 ft (Fig. 1). During the subsequent winter the population

declined, especially just below the soil surface and at depths below about 33 in. In the final tobacco season, November, 1966, to March, 1967, the earliest increase in the root-knot population occurred at depths of 9-12 in below the ridge top and was delayed in the ridge and at greater depths.

##### *Eragrostis curvula*/TOBACCO ROTATION

The increase in the *M. javanica* population under *E. curvula* during the latter part of the 1965-66 season was very slight, compared with that which occurred under *T. minuta* (Fig. 2), and was not obvious in the top layers of soil. The build-up of the population to high levels under the final tobacco crop occurred later in the season than in the *T. minuta* rotation.

##### CONTINUOUS TOBACCO

The population of *M. javanica* at the start of the sampling period was much larger than under the other treatments (Fig. 3). The winter decline in the upper layers of soil was not to such low levels, and the build-up under the tobacco crops took place early in both seasons sampled. The decline of the population in the lower layers of soil in winter was more rapid and to a greater extent than in the upper layers.

In all three treatments the effect of ridging can be clearly seen (Figs. 1-3); the top 9-12 in of soil was virtually free of *M. javanica* before the tobacco was planted.

##### SOIL MOISTURE AND RAINFALL

The soil moisture patterns under all three treatments were very similar, so only those for continuous tobacco are presented (Fig. 4). The greatest variation in soil moisture occurred in the top 3 in of soil with wide fluctuations recorded, even at weekly intervals. At greater depths weekly fluctuations were less marked. The soil moisture pattern in the top 3 in of soil corresponded closely with the rainfall pattern (Fig. 4). The increase in soil moisture in deeper layers of the soil was delayed, not noticeably increasing at a depth of 5 ft until about one month after the onset of the rains and the initial increase in the top 3 in of soil. It was not until March of 1966 and 1967 that peak moisture-levels were recorded at these depths. The soil dried out throughout the dry season, from April, 1966, particularly in the top 3 in, where mois-

FIG. 1.—VERTICAL POPULATION OF *M. JAVANICA* (1961) AT EACH SOIL DEPTH (INCHES) UNDER *T. MINUTA* AND CONTINUOUS TOBACCO.



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FIG. 1.—VERTICAL DISTRIBUTION OF *MELOIDOGYNE JAVANICA* UNDER LAST TWO YEARS OF THREE YEARS *TAGETES MINUTA*/TOBACCO ROTATION, AUGUST, 1965—MARCH, 1967. INDEX VALUES 0-100 (DAULTON AND NUSBAUM, 1961) AT EACH SOIL DEPTH OBTAINED BY ASSESSMENT OF *M. JAVANICA* INFECTION OF TOMATO INDICATOR PLANTS

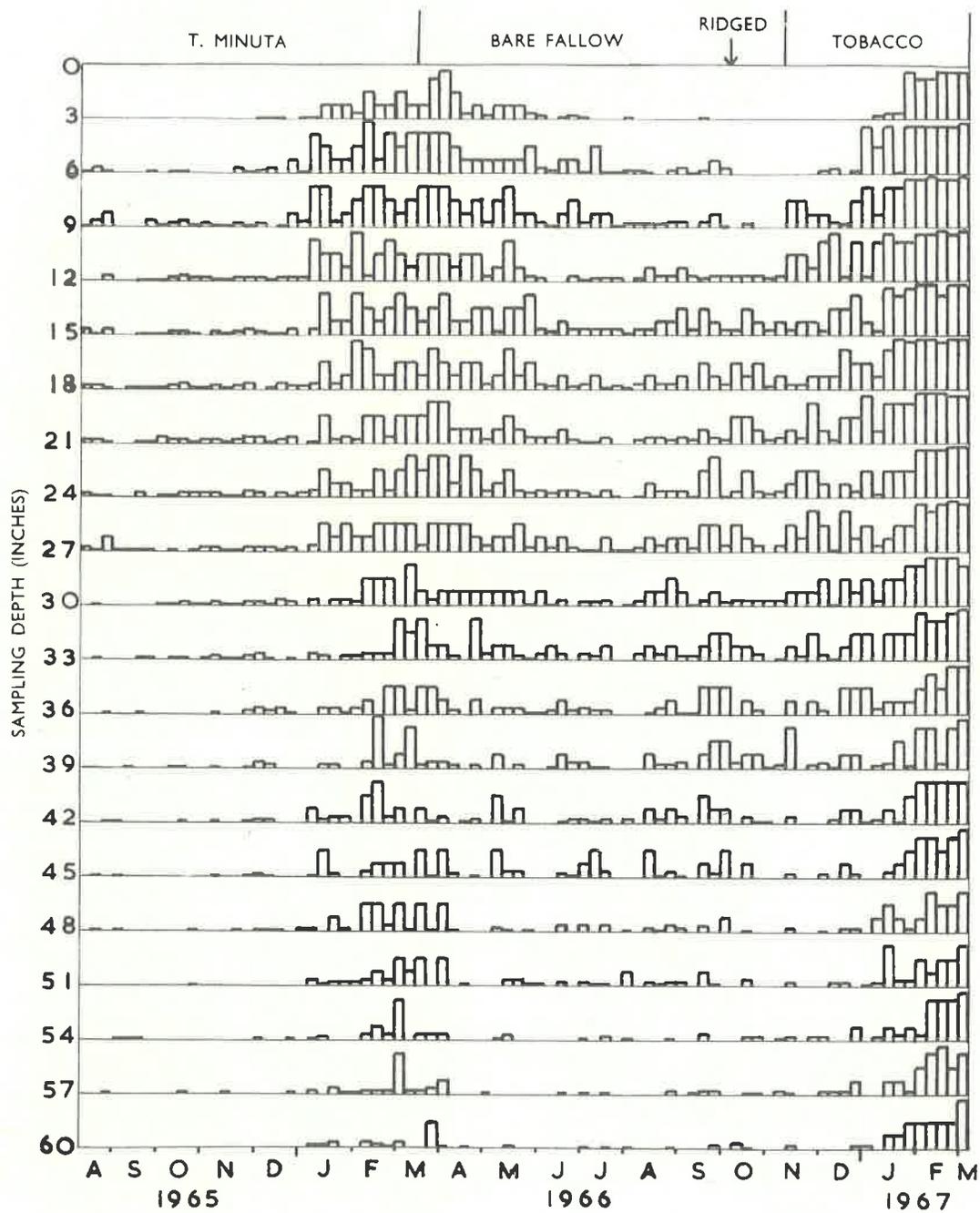


FIG. 2.—VERTICAL DISTRIBUTION OF *MELOIDOGYNE JAVANICA* UNDER LAST TWO YEARS OF THREE YEARS *ERAGROSTIS CURVULA*/TOBACCO ROTATION, AUGUST, 1965—MARCH, 1967. INDEX VALUES 0-100 (DAULTON AND NUSBAUM, 1961) AT EACH SOIL DEPTH OBTAINED BY ASSESSMENT OF *M. JAVANICA* INFECTION OF TOMATO INDICATOR PLANTS.

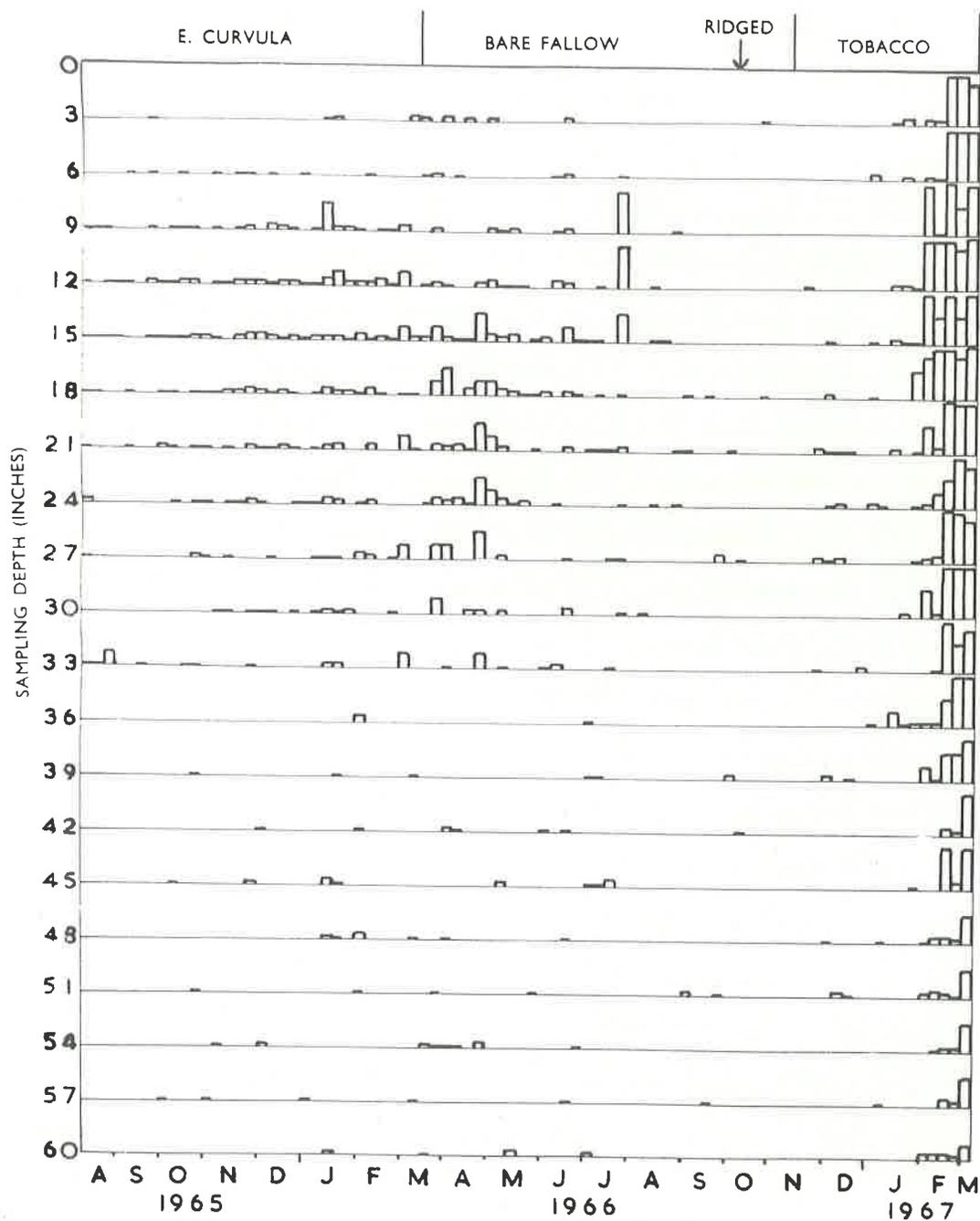


FIG. 3.—VERTICAL DISTRIBUTION OF *MELOIDOGYNE JAVANICA* UNDER LAST TWO YEARS OF THREE YEARS *ERAGROSTIS CURVULA*/TOBACCO ROTATION, AUGUST, 1965—MARCH, 1967. INDEX VALUES 0-100 (DAULTON AND NUSBAUM, 1961) AT EACH SOIL DEPTH OBTAINED BY ASSESSMENT OF *M. JAVANICA* INFECTION OF TOMATO INDICATOR PLANTS.

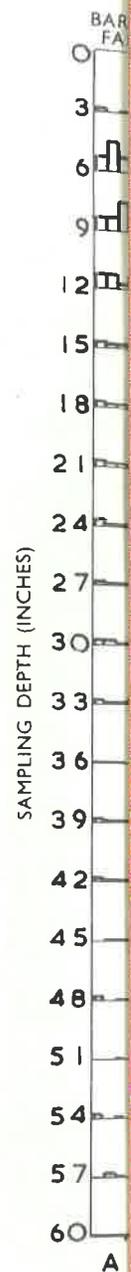


FIG. 3.—VERTICAL DISTRIBUTION OF *MELOIDOGYNE JAVANICA* UNDER LAST TWO YEARS OF CONTINUOUS TOBACCO, AUGUST, 1965—MARCH, 1967. INDEX VALUES 0-100 (DAULTON AND NUSBAUM, 1961) AT EACH SOIL DEPTH OBTAINED BY ASSESSMENT OF *M. JAVANICA* INFECTION OF TOMATO INDICATOR PLANTS.

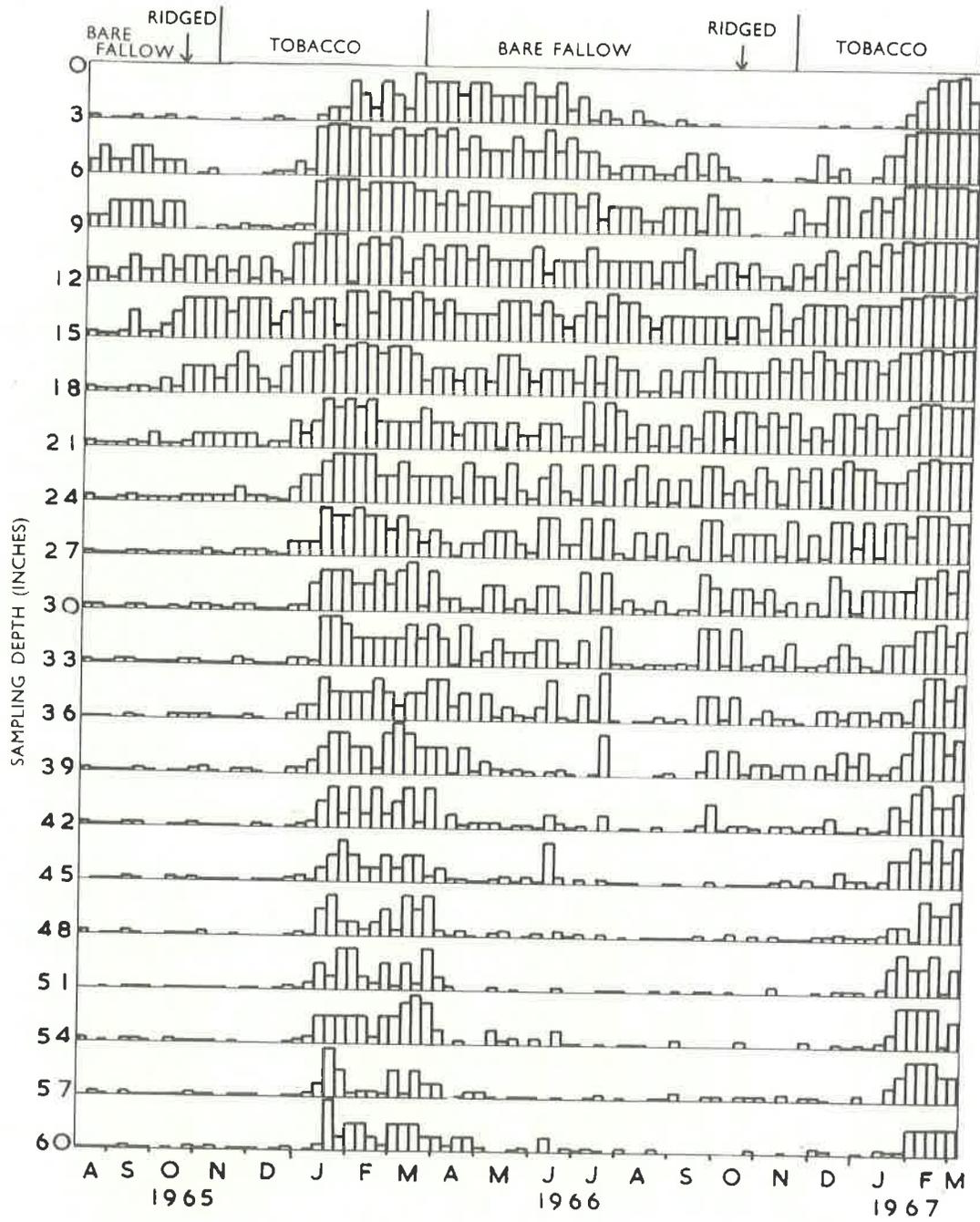
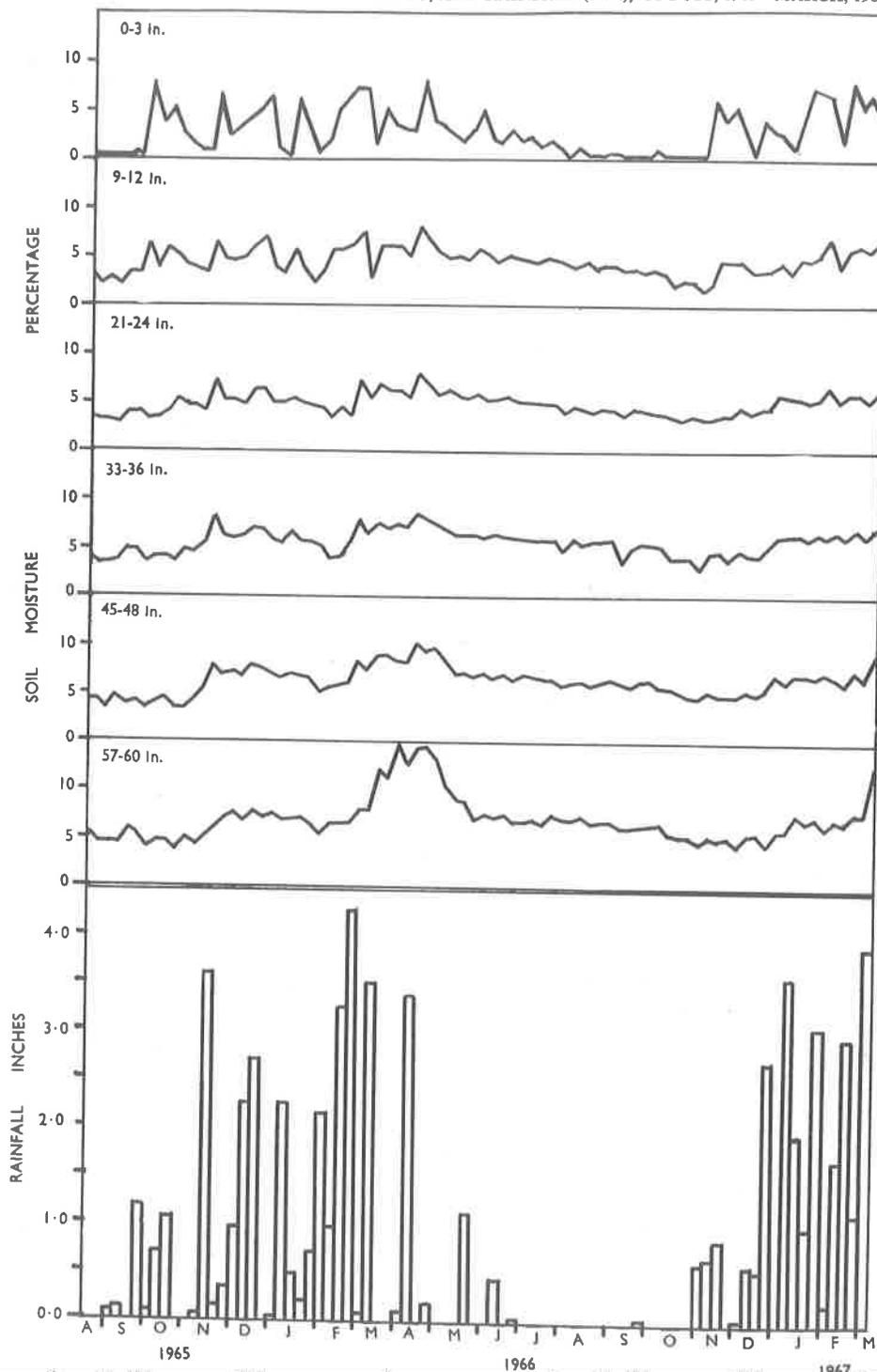


FIG. 4.—WEEKLY SOIL MOISTURE PERCENTAGE AT 0-3 IN., 9-12 IN., 21-24 IN., 33-36 IN., 45-48 IN., AND 57-60 IN., UNDER LAST TWO YEARS OF CONTINUOUS TOBACCO, AND RAINFALL (INS.), AUGUST, 1965—MARCH, 1967.



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ture dropped to less than 1.0 per cent. and was as low as 0.16 per cent. between August and November, 1966. At lower soil-levels it dried less.

The *M. javanica* population in soil allowed to dry out decreased more rapidly than in moist soil under laboratory conditions (Table 1). After two weeks the soil moisture fell to levels similar to those observed in the top 3 in of soil in the field in late winter and early summer, resulting in a depletion of the population.

#### SOIL TEMPERATURE

The highest temperatures during the

summer months, between August and February, which are those likely to be critical to the survival of the nematodes, are shown in Table 2.

During the 1965-66 summer the effect of shading by the grass in the *E. curvula*/tobacco rotation was noticeable. The highest temperatures recorded during the same periods at a depth of 4 in were about 95°F during the 1965-66 summer, except under *E. curvula*.

Under laboratory conditions *M. javanica* populations were depleted at temperatures above 105°F in dry soil and above 110°F in damp soil (Table 3).

TABLE 1.—THE EFFECT OF SOIL MOISTURE ON A POPULATION OF *Meloidogyne javanica* UNDER LABORATORY CONDITIONS

Treatment time (weeks)	Air-drying soil			Moist soil		
	Soil moisture	<i>M. javanica</i> larvae	Root-knot infection index	Soil moisture	<i>M. javanica</i> larvae	Root-knot infection index
0	6.31%	70	8.3	4.11%	85	8.3
1	1.08%	25	10.0	4.15%	53	10.0
2	0.23%	4	1.0	5.36%	90	5.0
3	0.13%	3	0.7	5.97%	60	6.7
4	0.24%	1	0.3	7.38%	51	6.7

TABLE 2.—THE HIGHEST SOIL TEMPERATURES (°F) RECORDED IN EACH TREATMENT AT 2 IN DEPTH BETWEEN AUGUST AND FEBRUARY OF 1965-66 AND 1966-67

Treatment	1965-66						
	A	S	O	N	D	J	F
<i>T. minuta</i> /tobacco	97.0	105.5	107.5	108.5	101.0	104.5	87.5
<i>E. curvula</i> /tobacco	88.0	90.5	92.5	94.5	88.0	91.5	85.0
Continuous tobacco	98.0	105.0	98.5	108.0	105.0	110.0	100.0
Treatment	1966-67						
	A	S	O	N	D	J	F
<i>T. minuta</i> /tobacco	86.0	97.0	114.5	110.0	103.0	88.0	86.5
<i>E. curvula</i> /tobacco	84.5	94.5	114.0	109.0	104.0	89.5	90.0
Continuous tobacco	88.0	97.0	109.0	106.0	100.0	90.0	92.0

TABLE 3.—MEAN NUMBERS OF *Meloidogyne javanica* SURVIVING HEATING TO TEMPERATURES BETWEEN 95°F AND 120°F FOR 10-MINUTE EXPOSURE PERIODS

Temperature (°F)	A. Soil allowed to dry while heating		B. Soil kept damp while heating	
	<i>M. javanica</i> larvae	Root-knot infection index	<i>M. javanica</i> larvae	Root-knot infection index
95	62	6.7	168	10.0
100	80	8.3	132	8.3
105	60	8.3	101	10.0
110	15	2.3	125	10.0
115	9	0.3	12	0.3
120	0	0.0	3	0.3

The populations used in treatments A and B were not comparable in size.

#### DISCUSSION

Under all treatments, the bulk of the *M. javanica* population was in the upper 24 in of soil; there were fewer at greater depths but some were still found down to 5 ft. Distinct seasonal fluctuations in the population were seen, with a build-up during the late summer months and a decline in winter. During January to March, 1966 and 1967, there was a great increase in the *M. javanica* population in the lower depths. Since there were few, if any, roots in this region in these experiments, it seems likely that nematodes were carried down by the heavy rainfall occurring at the time. Downward movement of nematodes with percolating water is known to occur in sandy soils in Florida (Ducharme, 1955). In the present experiments the nematodes were probably carried down mainly in the egg stage, because there was no similar increase in *M. javanica* larvae found by soil extraction techniques at these depths (Ferris, 1968).

It is likely that the rapid decline of the population in the lower levels was because the soil was very moist, the water-table being at about 5 ft in late February and March. Brain (1937) reported that in water-logged soil all stages of the root-knot nematode were destroyed in 60 days. Wallace (1968) has shown that low aeration in soil owing to waterlogging or depth may be lethal to eggs in the stage of embryonic development. Van Gundy, Bird and Wallace (1967) showed that these conditions maintained infectivity of larvae by inducing quiescence. These reports support the theory that the population in the lower depths of the soil consisted largely of eggs and explain the rapid decline.

Daulton (1951) found that, in a sandy soil with a heavy clay subsoil at 18 in, the majority of the *M. javanica* population inhabited the top 15 in and none were below 25 in. The present studies have shown that in deeper sandy soils *M. javanica* can survive at 5 ft for limited periods, presumably because movement is easier and soil aeration is greater. Wallace (1958 a, b) showed that *Heterodera schachtii* larvae migrated vertically more readily through soil of larger particle size. Sleeth and Reynolds (1955) found that infestation of *Sesbania exaltata* by *M. javanica* was extremely light in a fine-textured soil and much heavier in a coarse-textured.

According to Wallace (1956), it was generally considered that nematode damage to crops was most serious on sandy soils; he pointed out that these were better aerated because their pore spaces were larger. He also suggested that soil aeration is the most important single factor, associated with soil structure, that influences larval emergence, and that the rate of larval emergence of *H. schachtii* was decreased by increasing the clay content of a sandy soil.

The greatest daily and seasonal fluctuation of climatic conditions occurred in the upper layers of soil, particularly the top 3 in. It is difficult to separate the effects of soil temperature and soil moisture on a population of nematodes under field conditions. However, laboratory studies have shown that, in soil moisture and temperature conditions similar to those experienced in the field in late winter and early summer in Rhodesia, populations of *M. javanica* are reduced. Both egg and larval stages were substantially reduced by temperatures above 105°F, in dry soil, even over exposure periods as short as 10 min. Soil temperatures in this range were recorded at a depth of 2 in under the *T. minuta*/tobacco rotation and the continuous tobacco in the early summer of 1965 and under all treatments in 1966. Daulton and Nusbaum (1961) showed that about 8h exposure of *M. javanica* eggs from a Rhodesian population to temperatures of 97°F in dry soil reduced their viability to extremely low levels. It seems reasonable to assume that repeated shorter exposures to similar temperatures, as occurs under natural conditions, might have a similar effect. In the early summer of both seasons soil temperatures above 97°F at 2 in depth were frequently recorded except under *E. curvula*.

Laboratory studies showed that less than two weeks exposure of a population of *M. javanica* to a soil moisture-level similar to that in the top 3 in of soil in the field, for at least two months during late winter and early summer, seriously depleted the population. Because moisture is low and temperature high in the top 3 in of soil it is virtually free of *M. javanica* by late October and early November, when tobacco is planted, as was found by Jack (1944).

The decline of the *M. javanica* population in the top 3 in of soil to almost negligible levels becomes particularly significant when the land is ridged for tobacco planting.

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Since tobacco ridges are prepared from the top 3 in of soil in October, they provide a 9-12 in depth of soil virtually free of *M. javanica* in which the plant may become established. This provides a distinct advantage over planting on flat land. However, tobacco seedlings are planted in a 6 in deep hole and the initial downward growth of the roots is into the most heavily infested region of the soil, 9-24 in below the top of the ridge.

In a heavily infested soil, roots will rapidly become invaded by *M. javanica* and rendered useless to the plant. Most of the useful roots will then be confined to the ridge itself and will be subject to the fluctuating soil moisture conditions occurring there, resulting in wilting, poor growth and loss of yield. Here the benefit of soil fumigation is apparent. Daulton (1964) stated that soil fumigation under Rhodesian conditions clears nematodes from the soil in an area approximately 9 in in radius from the point of injection. Placement of nematicides at 12-15 in below the top of the ridge gives the plant at least another 12 in of relatively uninfested soil in which to become established during its early growth.

Under the three-year *E. curvula* rotation a slight increase in the *M. javanica* population was seen at the end of the summer of 1965-66. Since *E. curvula* is a shallow rooting plant, with most of the root system confined to the top 9 in of soil, any build-up of *M. javanica* from reproduction on the grass could be expected to occur in this region. However, since the increase occurred mainly between 9 and 24 in and was similar in size and distribution to that under bare fallow in the same experiment (Ferris, 1968), it seems likely that it was because the nematodes reinvaded the area or moved in with soil moisture from more heavily infested surrounding plots.

Oostenbrink (1960) reported that *Tagetes patula* reduced soil populations of *Meloidogyne hapla* significantly compared with other crops. Daulton and Curtis (1963) showed that, under greenhouse conditions, entry of *M. javanica* larvae into the roots of *Tagetes minuta* was inhibited, and those that did enter failed to develop, and the nematode population declined to very low levels. Under field conditions in Rhodesia the population of *M. javanica* declined less under *T. minuta* than under *E. curvula*. They also appeared to reproduce during

the late summer of 1965-66 because the population increased under the *T. minuta* treatment more than under *E. curvula* or bare fallow (Ferris, 1968). This cannot be accounted for purely by reinvasion from more heavily infested surrounding areas. *M. javanica* increased in numbers in the upper layers of soil in the vicinity of the root systems of the plants, indicating that some reproduction occurred on *T. minuta*. Martin (1958) found small numbers of galls on the roots of *T. minuta* under field conditions in Rhodesia.

In all treatments the *M. javanica* population increased to high levels under the final tobacco crop. The rate of increase depended on the initial population levels in the soil at the time of planting. In the continuous tobacco treatment, where the population was already fairly high, reinvasion of the ridge from surrounding areas could occur quickly, and the tobacco roots were attacked very soon after planting, before the seedlings had become well established. Reinvasion of the tobacco ridge after three years of *E. curvula* was much slower, because there were few nematodes in the surrounding soil, so the population increase was only seen at the end of the season, when most of the growth of the tobacco had already taken place.

The findings in these studies tend to support the suggestions of Wallace (1963) and Wallace and Greet (1964), that the static rather than the dynamic concept applies to the vertical distribution of nematodes. According to the former concept, there is a differential reproductive rate with depth, depending on the distribution of food, root abundance, soil moisture, soil type, aeration and soil temperature. This results in a nematode species being most numerous in the zone at which conditions for its reproduction are most favourable, rather than there being a physical migration to a more favourable zone.

However, some movement of nematodes in the soil, either active or passive, obviously does occur, but this is probably of less importance in terms of population increase at different depths than differential reproductive rates. The static concept might be modified by adding that, besides there being a differential rate of reproduction with depth, there is a differential rate of mortality, also dependent on the environmental conditions, and that it is largely the combined effect of

these two factors that determines the vertical distribution of nematodes.

#### ACKNOWLEDGEMENTS

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