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Studies on the Life-history and Habits of the Burrowing Nematode, *Radopholus similis*, the Cause of Black-head Disease of Banana

CLIVE A. LOOS*

The burrowing nematode, *Radopholus similis* (Cobb, 1893) Thorne, 1949, is an important pest of cultivated bananas in Central America and the West Indies. The pest invades the root system and causes lesions which may girdle and destroy roots up to one-half inch thick. Heavily infected plants are stunted, carry small fruit and topple over easily because of inadequate root anchorage (Loos & Loos, 1960 a). Large numbers of *R. similis* in all stages of development may be found in lesions in both root and rhizome cortical tissue. Since bananas are propagated by rhizomes, planting material is mainly responsible for wide-scale dissemination of the pest (Loos & Loos, 1960 b). Individual specimens, used in these studies, were obtained from rhizome lesions in Jamaica.

MORPHOLOGICAL AND POPULATION STUDIES

Lacatan, Robusta and Gros Michel are three of the chief banana varieties grown for export purposes. No significant morphological differences were observed in burrowing nematode populations collected on these three varieties at various times and places. Size range was so considerable that it left no doubt that to attempt separation of populations between numerous banana varieties, on a size factor, was not possible. Van Weerdt (1958) made similar observations for *R. similis* on citrus, corn and banana in Florida.

Burrowing nematodes, on extraction from banana tissues, are sluggish but may be stimulated to activity by passing air through the nematode suspension. On the other hand, individuals recovered from soil are active; this is understandable since those individuals were not from sedentary feeding positions but in active search for a host root. Ratios of males to females in lesions vary considerably; in large lesions, where extensive colonies had been built up, this ratio is generally in the proportion of 1.5 females to a male.

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Table 1. Egg-laying of gravid and large selected females of *Radopholus similis* in spots of distilled water.

Type	No. of Females	Eggs laid in water in 0-24 hours	24-48 hours	2-10 days
Gravid females	16	42	3	0
Large non-gravid females	34	6	0	0

EXPERIMENTS IN VITRO

EGG-LAYING: Females can be maintained from two to seven weeks in spots of distilled water on glass slides, provided they are transferred to fresh water every four to six days. An active specimen becomes sluggish a few hours after transfer but may again be induced to activity by raising it out of the water on the end of a needle for a few seconds until the film of water around its body evaporates, before replacement in the water spot.

A female may carry two eggs, one in each uterus; these eggs are generally laid in an unsegmented condition in a few hours though, due possibly to disturbance, change of environment or damage to the mother, it is not unusual for development to proceed to the four-cell stage before being deposited. A few cases occurred where eggs were not deposited but developed to the final pre-hatching stage in the uterus. In another instance a second egg formed in the anterior ovary developed up to the final pre-hatching stage but did not emerge. In all probability, in those cases, females were damaged but survived for many days. There were many instances too, where a gravid female died before laying and the egg was destroyed by bacteria. Females removed from banana lesions ceased egg production in under 24 hours though an occasional specimen laid at a much reduced rate on the second day (Table 1).

In another experiment 90 gravid females were transferred, in groups of 5 worms, to drops of fresh distilled water on glass slides and placed in damp chambers to avoid drying. During the first 24 hours mean egg-laying rate was 2.6 eggs per female. This is in close agreement with egg-laying of gravid females expressed in Table 1. None of the 90 females laid any more eggs over a 7 week observation period indicating that nutritional factors stimulated egg-laying.

At room temperature (75-90°F) larvae emerged from eggs, laid in water, from the fifth day onwards and all viable eggs were hatched in seven days. The majority of eggs hatched between the fifth and sixth days (Table 2).

EXPERIMENTS WITH LIVING ROOTS

Thick, fleshy banana roots are not suitable for accurate examination for endoparasitic nematodes. *Tephrosia candida,* a legume, was selected for these life-history studies since the seedling root is readily infected under laboratory

Table 2. Hatching of newly laid eggs of *Radopholus similis* in distilled water. Results based on viable eggs in eight batches.

	1	2	3	4	5	6	7	8	Total	% hatched
5 days	23	34	22	42	12	3	2	7	145	71.7
6 days	30	40	25	54	18	12	6	13	198	98.0
7 days	30	40	25	54	18	15	7	13	202	100.0

conditions, seedlings at a suitable stage of growth are readily available and their roots are most satisfactory for examination by methods described by Gadd & Loos (1941) and elaborated on in this paper. Temperatures in the laboratory, during the course of these experiments, ranged from 75-90°F.

INFECTION: A droplet of water was placed on a microscope slide and a solitary female, larva, or group of nematodes, depending on type of infection desired, transferred to the water. The pick-up and transfer needle was made with an eyebrow hair attached to the end of a dentist's pulp canal file with plastic cement, according to the manner described by Goodey (1957). Seedlings with straight radicles, 1½ inches in length, were obtained by planting seed in which germination had proceeded to the point where the radicle was just emerging in a pot of wet sand for a period of 24-48 hours at room temperature. The suitable seedlings were transferred to a dish of water, cleared of adhering sand particles with a soft brush and placed on a dry cloth or absorbent paper to remove excess water. Nematodes were placed in a small spot of water on a microscope slide and the seedling placed on it with the root tip resting in the water spot. If the spot of water was sufficiently small it was almost immediately drawn up around the root tip area and the nematodes brought into contact with the attractive root surface. Fine sand, which had passed through a 60 mesh sieve, was heaped lightly over the anterior one-half inch of the elongating root and dampened before the slide was placed in a damp chamber. Operations should be completed as quickly as possible, to avoid excessive drying with consequent damage to the root tip, and the slide left for 24-48 hours in a humid chamber before the infected seedling is planted to a pot of wet sand where it remains until time for examination. Addition of sand over the seedling root, though unnecessary as an aid to infection, is advisable to hold down the root tip from lifting prematurely from the slide and making twisted growth.

EXAMINATION: Females and larvae entered the root a short distance behind the tip. In under a week infection was observed as a faint discoloration which became more evident a week later. For examination purposes the seedling was

Table 3. Egg-laying and larval populations of gravid females of *Radopholus similis* in *Tephrosia candida* roots (Series 1)

	Number of females	Layers	Mean of layers	S.E. Mean
Eggs laid				
1 day	12	10	2.00	0.33
2 days	17	16	7.25	0.45
3 days	26	20	13.55	0.92
5 days	24	19	18.68	1.67
7 days	23	17	31.12	1.33
9 days	23	21	34.05	0.97
10 days	20	20	43.45	3.14
12 days	15	14	55.93	4.66
14 days	18	16	56.50	4.31
Larvae after				
7 days	23	17	0	0
9 days	23	21	4.5	0.26
10 days	20	20	9.25	0.63
12 days	15	14	15.14	1.12
14 days	18	16	18.44	1.21

carefully transferred to a dish of water, excised immediately beneath the cotyledons and the root cleared of adhering sand particles with the aid of a fine brush. Preferably at this stage, while the root is still in water, air is removed from the specimen tissues by means of a vacuum pump. Sufficient air was removed when roots sank on release of the vacuum. This air exhaustion was necessary since air bubbles in the tissues obscured accurate examination of cell contents. Roots cleared of sand and air were macerated in equal parts of 10 percent nitric and 10 percent chromic acids, maceration time depending on root thickness, though thirty minutes to one hour was generally found to be sufficient. Much of the dark orange stain of chromic acid, in the root tissues, was removed by washing macerated roots in tap water for about one hour. A root was sufficiently macerated when it flattened easily, without disintegrating, between a slide and cover slip on slight pressure to the slip. Microscopic examination was greatly facilitated when a macerated root was mounted in 10 percent caustic potash before a cover slip was applied and the specimen pressed flat. Caustic potash dissolves fat in nematode bodies and eggs but there is sufficient time for observation and counts of root contents before this occurs. The thick hypocotyl section of the seedling root was an effective holding place for transference of the root during preparation processes; this section is cut away with a sharp knife or razor blade at the final transfer immediately before placing a cover slip over the specimen.

After entry neither female nor larva travelled far. Generally a female was surrounded by her eggs; if she moved her track was recognized from the trail of eggs left behind. Consequently there was no difficulty in counting her offspring accurately during the first three weeks following infection. However, after that period eggs of the second generation became mixed with those of the original female to make accurate determination of individual efforts impossible.

Table 4. Egg-laying and larval populations of unselected females of *Radopholus similis* in *Tephrosia candida* roots (Series 2).

	Number of females	Layers	Mean of layers	S.E. Mean
Eggs laid				
1 day	32	11	2.00	1.41
2 days	28	7	2.86	0.74
3 days	28	23	7.91	0.69
4 days	24	24	11.75	1.04
7 days	26	25	29.12	1.90
9 days	19	19	36.53	3.13
10 days	26	25	36.44	3.12
11 days	28	25	34.72	3.61
12 days	17	15	45.93	5.21
14 days	17	17	50.06	3.34
17 days	13	13	53.00	6.94
Larvae after				
7 days	26	25	0	0
9 days	19	19	2.26	0.36
10 days	26	25	2.64	0.80
11 days	29	27	5.22	1.18
12 days	17	15	13.27	2.57
14 days	17	17	19.29	2.16
17 days	13	13	28.54	2.94

EGG-LAYING: Series 1.-Gravid females. In the first series of experiments only females with visible eggs (gravid) in the uterus were used for infection. Frequently, however, those eggs were deposited before worms entered a root. Though gravid females were selected to ensure that only actively laying worms would be used it did not ensure that they would continue to lay for even a week. In fact it was found that 14% of individuals causing infection did not lay any eggs and nearly as many laid very few eggs. The maximum number of eggs laid by any individual was 76 in 14 days. It was evident, therefore, that some selected worms were near the end of their egg-laying period at time of selection. A summary of examination results made between 1 and 14 days is given in Table 3.

Series 2.-Unselected females. In the second series of experiments no conscious selection of females was made though it is possible that, subconsciously, larger individuals were more frequently chosen since they were easier to pick up and less likely to be large larvae. The selections were finally viewed under a microscope to ensure that only adults were collected. At total of 258 females entered roots. Examinations made from 1 to 17 days are summarized in Table 4.

NON-LAYERS: Females referred to in Tables 3 & 4 originated from a population with a large number of males, and it is fair to assume that chances of picking unfertilized females for these experiments were, therefore, small. In series 1 (gravid females) 10 of 12 (83%) commenced laying within 24 hours and showed a mean of 2.0 eggs per layer; in series 2 (unselected, non-gravid females) in the same time period, only 11 of 32 (34%) laid and in this case too, the mean was 2.0 eggs per layer. Obviously layers of the unselected females in series 2 were in the gravid category but were picked up as unselected non-gravids since eggs had been deposited shortly before they were picked up. The great difference in numbers of non-layers in the two series (10% in gravid and 70% in unselected females) over a two-day period suggested a time lapse between adulthood and commencement of egg-laying. That this pre-egg-laying period was of short duration was demonstrated in egg-laying results of the unselected females on the third day; the percentage non-layers dropped and the mean eggs per layer rose significantly (Tables 4 and 5).

In the gravid females series there were worms which did not lay or laid only a few eggs at 3, 5 and 7 days after entry into roots. These females presumably completed egg-laying but survived for a period after reproduction ceased. There was no indication of a succession of egg-laying periods with rests between such periods.

MEAN RATE OF EGG-LAYING: The mean numbers of eggs found at each examination in Series 1 and 2 (gravid and unselected females) are indicated

Table 5. Egg-laying of gravid (G) and unselected non-gravid (NG) females in *Tephrosia candida* roots.

	Number of entries		Number of non-layers		Mean eggs Total entries		S.E. mean Total entries	
	G	NG	G	NG	G	NG	G	NG
Eggs laid.								
1 day	12	32	2	21	1.60	0.69	0.36	0.23
2 days	17	28	1	21	6.82	0.71	0.60	0.35
3 days	26	28	6	5	10.42	6.50	1.34	0.81
7 days	23	26	6	1	23.00	28.00	3.38	2.15

by a solid circle in Figs. 1 and 2. Straight lines which best fit the data are represented by equations $Y = -1.399 + 4.367x$ (gravid) and $Y = -0.8348 + 3.55x$ (unselected). Mean rates of egg-laying are 4.367 and 3.55 respectively over a two-week period. The higher rate for gravid females is attributed to higher egg production over the first three days after entry into a root. In both series it was apparent that egg-laying was proceeding unchecked beyond the observed two-week period.

Rate of hatching will be a reflection on the rate of egg-laying so long as incubation periods remain constant and all eggs hatch. Mean numbers of larvae found from 7-14 days are also shown in Figs. 1 and 2. Straight lines which best fit these observations are $Y = -19.1712 + 2.753x$ (gravid) and $Y = -21.7831 + 2.766x$ (unselected). Those mean hatching rates are in close agreement with each other (2.753 and 2.766) though somewhat less than corresponding egg-laying rates (4.367 and 3.55). Since the incubation period is constant the inference is that a fair proportion of eggs did not hatch. This inference is supported by van Weerdt (1960) who stated that a good percentage of eggs, particularly those slightly longer and narrower (length/width exceeding 2.5), more strongly bent and darker colored, failed to develop normally. Whether in the present instance a lower hatching rate is due to that factor or of non-fertilization was not clear.

RATE OF EGG-LAYING OF INDIVIDUALS: It will be realized that mean rates of

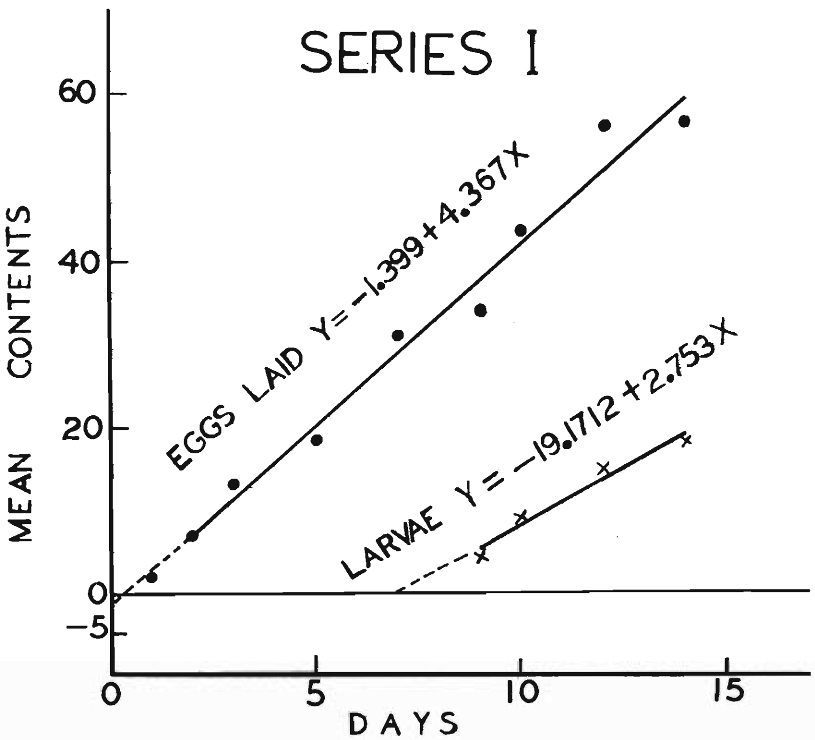

Fig. 1. Mean rate of egg-laying in *Tephrosia candida* by a population of gravid females from banana rhizome lesions and the mean rate of emergence of larvae.

egg-laying of a population give little indication of individual performances. Mean rate of a population over a period will normally be less than the mean rate of an individual unless all lay throughout the period. During 10 days in Series 1 (gravid females) 20 individuals laid 869 eggs giving an average daily rate of 4.34 eggs per individual. Of these, over that 10 day period, one laid 6, one 23 and another 31; it is possible that these individuals ceased egg-laying before the end of 10 days. The remaining 17 individuals laid from 34 to 64 eggs each with a mean daily rate of 4.76 over a 10 day period. This figure is probably fairly representative of the rate of egg-laying of individuals. Maximum rate observed was 6.4 eggs per day. Maximum rate observed in Series 2 (unselected females) was 7.7 eggs per day over a period of 9 days and maximum number laid by any one individual in 17 days, the longest period under observation, was 95 which amount, if she commenced laying on the first day, gives a mean of 5.6 eggs per day. These mean rates are in fairly close agreement to the maximum laid by a gravid female, in distilled water, over a 24 hour period.

INCUBATION PERIOD: It was previously shown that, *in vitro*, eggs may hatch in 5 days and that all hatchings were completed in 7 days. Eggs laid in roots take somewhat longer to hatch. Roots in Series 1 and 2 contained no larvae at the examination made after 7 days while larvae were observed, in some roots of both series, at the examination made after 9 days. Eggs from which these larvae emerged were probably laid shortly after females entered roots, in which case an incubation period, as observed, lies between 7 and 9 days.

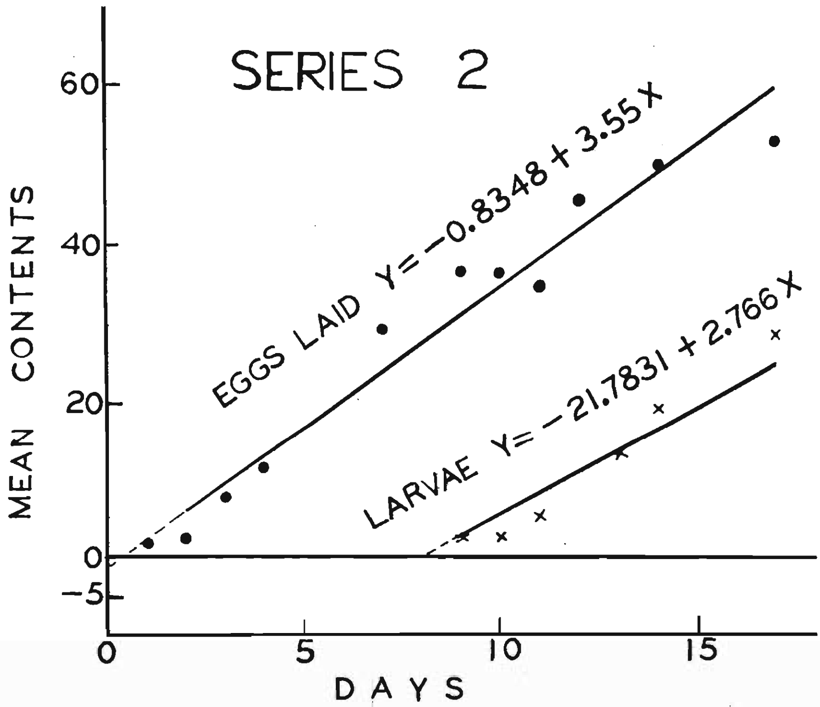

Fig. 2. Mean rate of egg-laying in *Tephrosia candida* roots by a population of unselected females from banana rhizome lesions and the mean rate of emergence of larvae.

A mean incubation period in roots may be derived from Figs. 1 and 2. If larval graphs are prolonged until they cut the X-axis, the points of intersection are 6.9 and 7.6 days for Series 1 and 2 respectively. We could conclude, therefore, that a mean incubation period for *R. similis* eggs, under the conditions of these experiments, was between 7 and 8 days.

LARVAL PERIOD: A direct estimate of the larval period was obtained by teasing roots, each of which had been inoculated with 10 recently hatched larvae, at daily intervals commencing after the ninth day. Results are set out in Table 6. Larval period was 10 to 13 days with the majority attaining adulthood in 11 days. Larval period for males was a day shorter than that for females.

PRE-EGG-LAYING PERIOD: Larvae becoming adult in 10 days did not, however, commence egg-laying until after the 12th day. Although it was not possible to determine with certainty the number of females concerned in the laying of those eggs, since the infected roots contained more than one female, the small number of eggs laid at the end of the 12th day suggested that they were laid by a single female. At the end of the 13th day egg-laying was a general feature and at the end of the 14th day 14 females had laid an average of 7.6 eggs per individual (Table 6). In comparison Gadd & Loos (1941) found that *Pratylenchus coffeae* had an adult pre-egg-laying period of 15 days.

FERTILIZATION AND EGG-LAYING: Gadd & Loos (1941) found a delay in commencement of egg-laying of unfertilized *Pratylenchus coffeae*. Two experiments were set up to ascertain if fertilization was a prerequisite to egg-laying of *R. similis* or if this species is parthenogenetic. In the first experiment 34 newly hatched larvae were inoculated, one to a root, and after 48 hours in a damp chamber the seedlings were planted to pots of wet sand. Six weeks later each of 20 positive infections contained a female without progeny. Under conditions of mass infection and colony existence egg-laying should have commenced in under 12 days and, assuming a continuous period of egg-laying, each female should have laid over 120 eggs. In a second experiment large juveniles were introduced, one to each seedling root. Sixteen days later, of 8 positive infections, 7 were females without progeny and one a male; of 10 positive infections examined 28 days after inoculation 8 were females without progeny, one a male and the other a female with 11 larvae and 67 eggs. The reason for this apparent single parthenogenetic case is not known. There is a possibility that it was a young fertilized female.

NUTRITION AND EGG-LAYING: *In vitro* studies suggested that egg-laying was governed by nutritional factors since separation of actively laying individuals from plant tissues to water caused egg-laying to cease in under 24 hours. That this cessation was due to lack of nutrition and not to disturbance caused by transfer was demonstrated in the following experiment.

Table 6. Larval and pre-egg laying periods of *R. similis* in *Tephrosia candida* roots.

Age of Days	Number nematodes	Juveniles	Females	Males	Eggs	Percentage Adults
9	21	21	0	0	0	0
10	11	7	0	4	0	57
11	15	1	10	4	0	93
12	22	2	16	4	4	91
13	16	0	13	3	52	100
14	20	0	14	6	107	100

From a collection of gravid females, recently obtained from rhizomes, 10 were inoculated to seedling roots and 60 transferred to distilled water on a glass slide. Forty-eight hours later 10 females in roots had laid 84 eggs (8.4 per female) while 60 females in water had laid 162 eggs (2.7 per female). Although the females in water were left for a further 10 days no more eggs were laid.

In a third experiment gravid females, which had ceased egg-laying over the previous 4 days of a five-day starvation period in water, were inoculated to *Tephrosia* roots. Results of examinations made 2, 3, 4 and 10 days after inoculation are expressed in Table 7. Those results are in close agreement with egg-laying of non-gravid females taken directly from banana roots (Table 4). The quick re-establishment of egg-laying of females, on transfer from starvation medium to root tissues, proved conclusively that egg-laying is correlated with nutrition.

MOLTS IN WATER: Large juveniles requiring but a single molt before adulthood completed it in water though, in many cases, they were unable to completely shed their cast cuticle. Juveniles requiring more than one molt before adulthood failed to make a second molt.

INFECTION OF ROOTS: All larval stages, from newly hatched second stage larvae to the fourth-stage pre-adult molt, are infective. Females moved in and out of roots at will but males were incapable of such movement. However, males feed in roots provided the final molt takes place in plant tissues. Fertilization occurs in the host tissues though there is no evidence that it cannot occur outside a root.

LIFE CYCLE: Life cycle, egg to egg, at temperatures ranging between 75° and 90°F, of *R. similis* in roots of *Tephrosia candida* was completed in 20-25 days; that period may be divided into 8-10 days for eggs to hatch, 10 to 13 days as larval period and 2 days as adult before egg-laying commences. The life cycle period agrees closely with Suit and DuCharm's (1957) estimate of 3-4 weeks for *R. similis* in citrus roots. Van Weerdt (1960) recorded 4 larval molts, the first occurring in the egg. The 3 molts outside the egg, occur during 10-13 days. The fourth larval or pre-adult stage is the shortest of the larval periods and there is no apparent increase in body length at that time.

Table 7. Egg-laying of single gravid *Radopholus similis* females introduced to *Tephrosia candida* seedling roots after a 5 day starvation period in water during which time egg-laying ceased.

	Egg Contents in Root After—			
	2 days	3 days	4 days	10 days
Degrees of freedom	6	7	7	6
Mean per root	2.5	8.1	12.1	31.0
Mean per root averaged per day	1.25	2.72	3.02	3.10
SEM	0.16	0.56	0.58	0.79

SUMMARY

No significant morphological differences were observed between populations of *Radopholus similis* from Lacatan, Robusta and Gros Michel banana varieties. The nematode, on extraction from banana tissues, is sluggish but may be stimulated to activity by passing air through the nematode suspension.

Gravid females when transferred from roots to water cease laying in under 24 hours. Egg-laying in water averaged 2.6 per female with a best individual performance of 6 eggs. Eggs laid in water hatch normally. A rapid method for infection and later determination of population in a seedling root is described. The value of this method in the study of the life cycle of *R. similis* is demonstrated. Females lay on an average of 3.5 to 4.6 eggs per day and continued laying beyond 2 weeks. Eggs hatch in from 5 to 7 days in water and 7 to 8 days in a root. The larval period is 10 to 13 days with the majority becoming adult in 11 days. There is a pre-egg-laying period of 2 days. Unfertilized females do not lay; there was evidence of a possible parthenogenetic case from over a large number of observations. Egg-laying of fertilized females is governed by nutritional factors. Removal of actively laying females from host tissues to water caused egg-laying to cease in under 24 hours. Reintroduction of those females to a host induced egg-laying to recommence. All larval stages and females are infective. Males are incapable of entering roots. Life cycle, egg to egg, is completed in 20 to 25 days which period may be divided to 8 to 10 days for eggs to hatch, 10 to 13 days for larval period and 2 days as adult before laying commences.

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Effect of Temperature on Hatching of *Aphelenchus avenae* Eggs*

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Aphelenchus avenae Bastian, 1865, is a common soil-inhabiting nematode. Although frequently associated with plant parts, it is not considered to be an obligate parasite of higher plants, according to Steiner (1936). Since Christie and Arndt (1936) reported that this species feeds like plant-parasites and since it can be rapidly increased in the laboratory, *A. avenae* may become important in the study of nematode physiology, ecology, and genetics. This nematode may also be useful in screening chemicals for nematocidal activity because of these characteristics.

Little has been published on the hatching of eggs in the Tylenchida. Dropkin, et al. (1958) reported that the stylet of *Meloidogyne arenaria*

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