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Stage-specific Population Development and Fecundity of *Paratrichodorus minor*[1]

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Abstract: A conceptual model of the life cycle of *Paratrichodorus minor* consisting of the egg stage, four juvenile stages, and the adult stage was proposed. Development of an individual from one stage to the next was described by a probability distribution defined by the mean length of time spent in the stage and the standard deviation associated with the mean duration. Experiments were conducted to estimate stage durations, stage-specific survivorships, and a fecundity rate for females. Eggs hatched on agar plates at a mean time of 53.3 ± 7.3 degree-days using a basal threshold of 10 C (DD_{10}) with a range of 40–64 DD_{10} after deposition. Forty-five percent of the eggs observed ultimately hatched. Of the eggs that died, 44% died before the nematode form could be observed in the egg and 56% died after movement had been observed. First generation population peaks following inoculation with first-stage juveniles occurred at 28 DD_{10} for second-stage juveniles, 67 DD_{10} for third-stage juveniles, 109 DD_{10} for fourth-stage juveniles, and 143 DD_{10} for adults. Adult males are rare and were never observed in these studies. The fecundity rate was 0.784 eggs/(female·DD_{10}^{-1}), but the maximum length of the egg-laying period was not determined. The minimum egg-laying period was 73–113 DD_{10}, and minimum egg production was 57–86 eggs per female. The preovipositional period for adult females was estimated to be 79 DD_{10}. In the presence of a host, total population numbers increased, but in the absence of a host, the population declined to 33% of the initial level after 300 DD_{10}.

Key words: Paratrichodorus minor, population dynamics, fecundity.

The stubby-root nematode, *Paratrichodorus minor* (Colbran, 1956) Siddiqi, 1974, was first reported to be an important agricultural pest in 1951 (6). It has a wide host range, including plants from more than 40 genera (2,7,14,16,18). Completion of the life cycle of *P. minor* required 16–17 days at 30 C (320–340 DD_{10}), 17–18 days at 27 C (289–306 DD_{10}), or 21–22 days at 22 C (252–264 DD_{10}) (5,10,12). Hatch occurred within 100–120 hours at 22 C or 5–6 days at 21 C after eggs were laid (2,3). Morton (9) followed development of the population through each life stage as differentiated by the development of the gonad primordia. No corrections were made for extraction efficiency which biased the results against those stages less efficiently extracted.

A conceptual model for a simulator of the life cycle of *P. minor,* an ectoparasitic nematode, consisting of an egg stage, four juvenile stages, and an adult stage is proposed (Fig. 1). The current research was undertaken to generate the data from which the model parameters could be estimated. Some parameters were calculated directly from the data obtained, whereas others were estimated using analytical techniques presented elsewhere (15). The goals of this study were 1) to determine the mean and standard deviation for the length of time from egg deposition to egg hatch, 2) to generate age-structured population data following inoculation with a uniform age cohort of first-stage juveniles, 3) to determine the fecundity rate of females, and 4) to determine population dynamics in the absence of a host.

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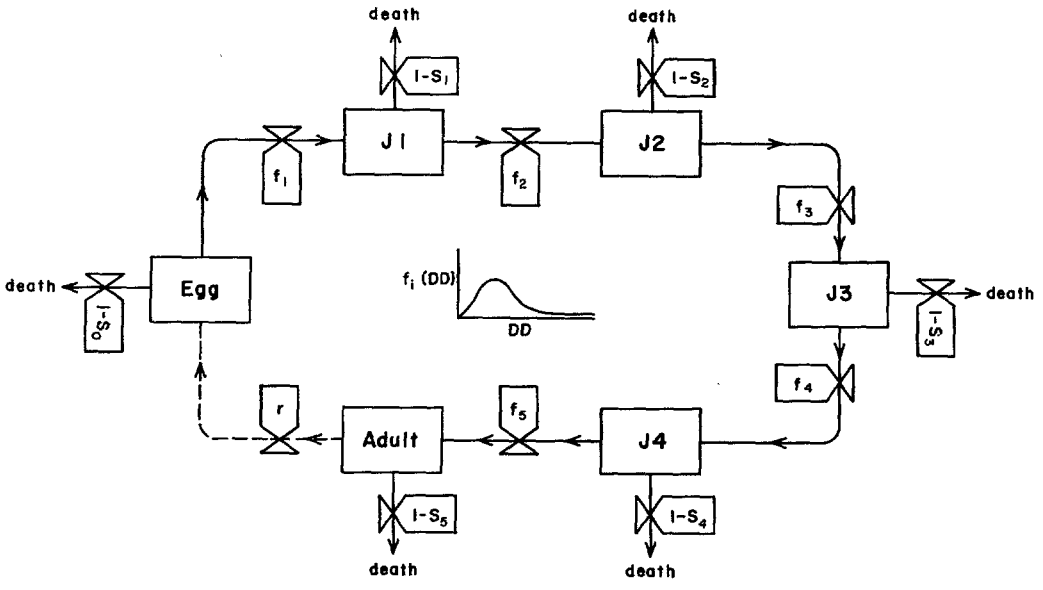

FIG. 1. Conceptual model for the life cycle of *Paratrichodorus minor*. Maturation of an individual from one stage to the next is described by an Erlang distribution, f(DD), defined by a mean and standard deviation for the stage duration. A proportion ($1 - S_i$ of the individuals in each stage die before maturing to the next stage. The rate of egg production is r.

MATERIALS AND METHODS

Physiological (based on degree-days), rather than chronological, time was the independent variable in this model. One degree-day using a basal threshold of 10 C (DD_{10}) represents 1 day at 1 degree over the threshold or 1 day at 11 C. Not all individuals in a population of the same age mature at the same time. The Erlang distribution, used to describe the maturation of an individual from one stage to the next stage (8), is described by the equation:

$$f(t) = (\bar{x}/K)^{-K}(t)^{K-1} \cdot \exp[-Kt/\bar{x}]/(K-1)!$$

where t is the independent variable, in this case DD_{10}, $\bar{x}$ is the mean length of time spent in the stage, and $K = \bar{x}^2/\sigma^2$ where σ is the standard deviation associated with the mean. This function is completely defined by the mean length of time spent in the stage and the standard deviation. The life-stage model also requires values for stage-specific survivorship (S_i) and fecundity rate (r) for adult females. Males of *P. minor* are rare; therefore, males are not included in the proposed model. The following experimental methods were designed to parameterize this model.

Egg development: Seed of sudan grass *Sorghum sudanense* (Piper) Stapf cv. Piper were surface sterilized by soaking in 0.5% sodium hypochlorite for 10 minutes and rinsed with running tap water for 15 minutes. The seed were germinated on 0.6% water agar in petri dishes. Seedlings were maintained in a growth chamber at 27 C until root systems were well established. Greenhouse cultures of *P. minor* were maintained on sudan grass. The inoculum was extracted by rinsing the soil and root mass in water and catching the adult females of *P. minor* on sieves with 140 and 74-μm openings. Fifty gravid females were hand picked into a watch glass, rinsed three times with sterile water, and pipetted onto the agar. The petri plates were wrapped in aluminum foil and returned to the growth chamber. The plates were observed three times a day at 15× magnification using a 4 × 4-mm grid pattern on the bottom of petri dishes to assist in locating specific eggs for observation. Location, time of appearance, and developmental progress were recorded for each

egg until the egg hatched or decomposed. The length of time required to hatch was calculated as time of hatch minus time of deposition. Time of deposition was the mean between time of first appearance and the previous observation time unless the developmental state of the egg indicated one of the actual observation points was a more accurate choice. For example, if an egg was first observed at 16 DD_{10} and the previous observation was at 12 DD_{10}, the time of deposition was specified as 14 DD_{10}. If the egg appeared newly laid (i.e., a one-celled or two-celled egg), 16 DD_{10} was chosen as the time of deposition instead of 14 DD_{10}. Time of hatch was calculated in the same manner as time of deposition.

Juvenile development: Glass tubing (1 cm outside diameter) was cut into 12.7-cm lengths, covered at one end with fine mesh polyester cloth to confine plant roots, and filled with sterilized loamy sand (87% sand, 11% silt, 2% clay). Thirty tubes were embedded to a depth of 10.8 cm in loamy sand in each of 16 self-watering pots (Natural Spring, Planter Technology, Mountain View, CA) (Fig. 2) and maintained in a growth chamber at 27 C. Soil moisture was controlled by the depth at which the sensor was buried. Two sudan grass seeds placed in each tube were covered with a 0.6-cm layer of steamed soil. After germination, a single seedling was retained in each tube. Greenhouse cultures of *P. minor* were maintained on sudan grass. Mature females were extracted as described for the egg development experiment. The females were placed in the soil around the roots of established sudan grass plants, and the pots were placed on heating mats. A soil temperature of 27 C was maintained for 5 days to allow the females to feed and reproduce and for the first-stage juveniles (J1) to hatch from the eggs. The soil and root mass were rinsed in water, and the adults were removed using sieves with openings of 140, 74, and 43 μm. Soil and J1 which passed through the coarser sieves were caught on 38 and 25 μm opening sieves. The nematodes were separated from the soil using Baermann funnels. Some contamination

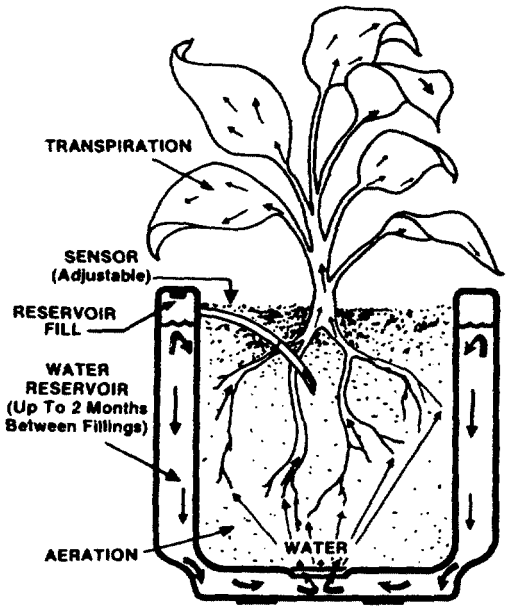

FIG. 2. Natural Spring self-watering pot.

with second-stage juveniles (J2) and adults was unavoidable. Two weeks after planting, each tube was inoculated with *P. minor* in 1 ml water using a syringe and canula with two holes, one each at depths of 1.2 and 3.4 cm. Each tube was then watered to close the inoculation hole. Ten samples were randomly taken during the inoculation process to determine the actual initial inoculum level. Each milliliter of inoculum contained 126 ± 13.4 J1, 5 ± 4.0 J2, and 11 ± 4.3 adults (A). Juvenile development classes (J1, J2, J3, J4) were designated according to the criteria established by Morton (9). Nematodes were extracted from 10 randomly chosen tubes after 1.5 hours (1.0 DD_{10}) to estimate the effective initial inoculum, i.e., the proportion of the initial inoculum that survived mechanical injury during the inoculation procedure. Soil and roots were rinsed from each tube and placed on separate Baermann funnels. After 48 hours, nematodes in 10 ml water from the funnel containing soil were combined with nematodes in 10 ml water from the funnel containing roots, counted by developmental stage, and corrected for stage-specific extraction efficiency. The stage-specific extraction efficiencies were

determined by using the experimental procedure to extract a population of known size and age structure, then calculating the percentage recovered by dividing the number recovered by the known initial number. The extraction efficiencies for this experiment were 23% for J1, 16% for J2, 10% for J3, 19% for J4, and 14% for adults. Ten randomly chosen tubes were sampled approximately every 8 hours (5.6 DD_{10}) for the first 2 days and every 12 hours (8.4 DD_{10}) for days 3 to 24. Resulting population data were plotted against DD_{10}. The entire sample was extracted to avoid error introduced by subsampling. Self-watering pots minimized the variation in soil moisture both over time (from very wet immediately after watering to partially dry before watering) and among replications. All experimental units were maintained at a constant temperature of 27 C.

Fecundity: Glass tubes embedded in self-watering pots were prepared as in the juvenile-development experiment. Young females were obtained by placing gravid females onto established sudan grass plants maintained at 27 C. After 5 days (to allow for feeding, egg deposition, and egg hatch), the females and newly emerged J1 were extracted from the soil. J1 were placed in the soil around roots of established sudan grass plants which were maintained in a growth chamber at 27 C for 8 days to allow them to reach the adult stage. The population of young females was extracted from the soil and used as inoculum. Each glass tube containing a 2-week-old seedling was inoculated with a single young female at a depth of 5 cm. Tubes were watered to close the inoculation hole. Ten tubes were sampled every 2 days (33 DD_{10}) beginning 7 days (121 DD_{10}) after inoculation and continuing for 14 days (352 DD_{10}). Soil and roots were washed from each tube and placed on separate Baermann funnels. Fifteen milliliters of water were removed at 3-day intervals from each funnel beginning 48 hours after the funnels were set up and continuing until no more nematodes were recovered. The procedure allowed sufficient time for eggs present in the soil to hatch. Mean numbers of progeny were calculated from those tubes with progeny. Mean numbers of progeny of the single female, corrected for extraction efficiency (38% for J1, 36% for J2, 45% for J3, 38% for J4, 41% for A), were plotted against physiological time (DD_{10}) to determine a rate of egg production. Using linear regression techniques, a straight line was fitted to the data. The slope of the line was the change in the number of progeny/(female·unit time^{-1}) and was used to estimate the fecundity. The point at which the regression line intersected the time axis, estimated the length of the pre-oviposition period.

Presence or absence of host: Glass tubes in self-watering pots were prepared as described in the juvenile-development experiment, except that half of the tubes were not seeded to represent the absence of a host. Greenhouse cultures of *P. minor* were maintained on sudan grass. Soil and root mass were rinsed in water, and the nematodes were extracted using sieves with openings of 140, 74, 43, 38, and 25 μm. Nematodes caught on all screens were mixed together to obtain a mixed age-structure population. Tubes were inoculated as described for juvenile development with the following inoculum levels: 4 ± 4.90 J1, 13 ± 4.07 J2, 104 ± 33.22 J3, 28 ± 9.80 J4, and 45 ± 19.89 adults. After 1 hour, two tubes with plants and two without plants were extracted to determine the effective initial inoculum levels. Two tubes from each treatment were sampled at 67, 134, 200, and 300 DD_{10}. Nematodes were counted by developmental stage and corrected for stage-specific extraction efficiency. Population counts were plotted against DD_{10}.

Results

Egg development: Of 29 eggs observed, 13 (45%) hatched, and 16 (55%) died. Average time to hatch was 53.3 ± 7.3 DD_{10} with a range of 40–64 DD_{10}. The first-stage juvenile was observed at a mean time of 33.6 ± 6.2 DD_{10} and movement of the nematode within the egg at 40.5 ± 7.8 DD_{10}. Time of death was defined as that time at which no further development was

observed or attack by bacteria became obvious. Seven eggs (44%) died before reaching the first juvenile stage and nine eggs (56%) died after movement had been observed.

Juvenile development: Effective initial inoculum levels were 106 ± 52.1 J1, 4 ± 6.0 J2, and 9 ± 12.0 adults. First-stage juvenile numbers declined from the initial inoculum level (Fig. 3a) and remained at a low level until progeny of the original J1 hatched (Fig. 4a); J1 numbers increased at 220 DD_{10} and continued to increase throughout the study. An increase in J2 first occurred at 9 DD_{10}, numbers peaked at 28 DD_{10}, and decreased as individuals matured into J3 (Fig. 3b). A second small J2 population peak was observed at 150 DD_{10}. A rapid increase in J2 numbers occurred beginning at 230 DD_{10} as progeny of the initial J1 population matured to the J2 stage (Fig. 4b). Third-stage juveniles were first observed at 28 DD_{10}, numbers peaked at 67 DD_{10}, and declined as individuals matured into J4 (Fig. 3c). A slight increase in J3 numbers was observed from 160 to 250 DD_{10}, followed by a rapid increase as progeny of the initial J1 inoculum matured to this stage (Fig. 4c). Numbers of J4 increased as the initial inoculum matured, peaked at 109 DD_{10}, and declined as individuals matured to the adult stage (Fig. 3d). Numbers of J4 remained low throughout the study (Fig. 4d). The adult population increased as individuals in the initial inoculum matured to the adult stage, peaked at 143 DD_{10} (Fig. 3e), and remained stable throughout the experiment (Fig. 4e).

Fecundity: Two periods of increase of numbers of progeny, from 121 to 224 DD_{10}, and from 250 to 300 DD_{10}, were observed (Fig. 5). Gravid females, in addition to the single female used in the inoculation procedure, were first observed in one sample at 192 DD_{10} and were present in all samples by 224 DD_{10}. Data points after this time were not used in calculating the rate of egg production per female per DD_{10} because more than one female was contributing to the total progeny. The relationship between mean total progeny per single female and DD_{10} from 121 to 224 DD_{10} was

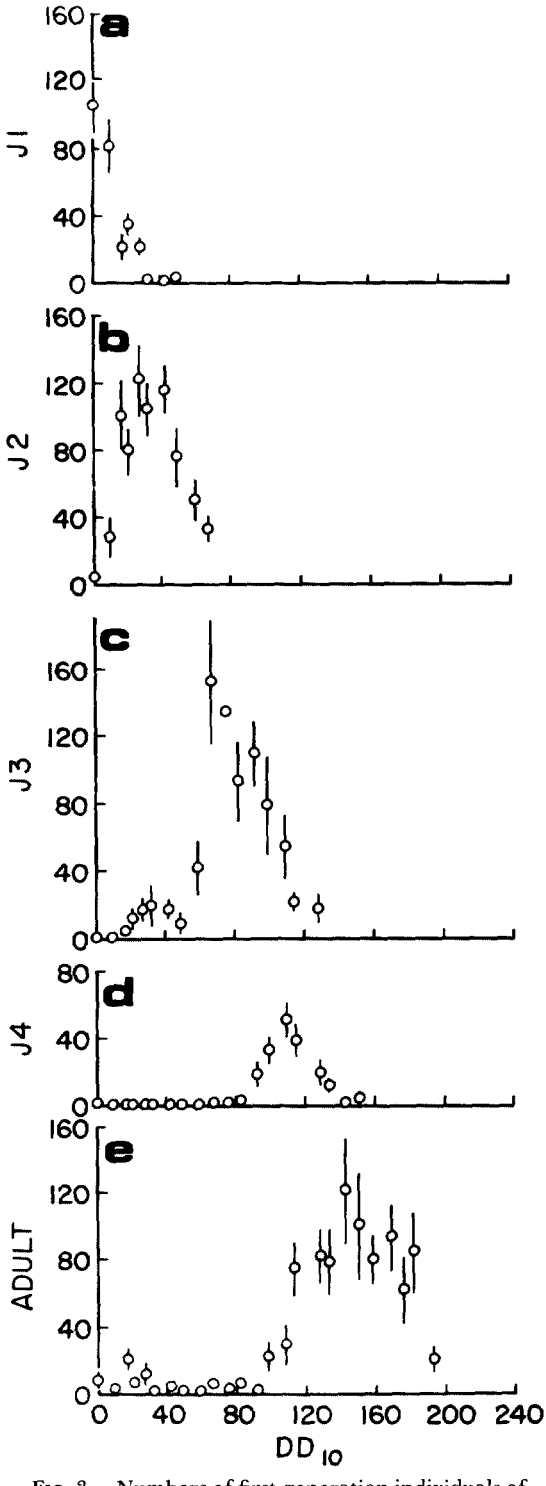

FIG. 3. Numbers of first generation individuals of *Paratrichodorus minor* in each developmental stage over physiological time, assuming a basal threshold of 10 C. Points are the mean of 10 replications, bars represent the standard error of the mean. a) First-stage juvenile. b) Second-stage juvenile. c) Third-stage juvenile. d) Fourth-stage juvenile. e) Adult.

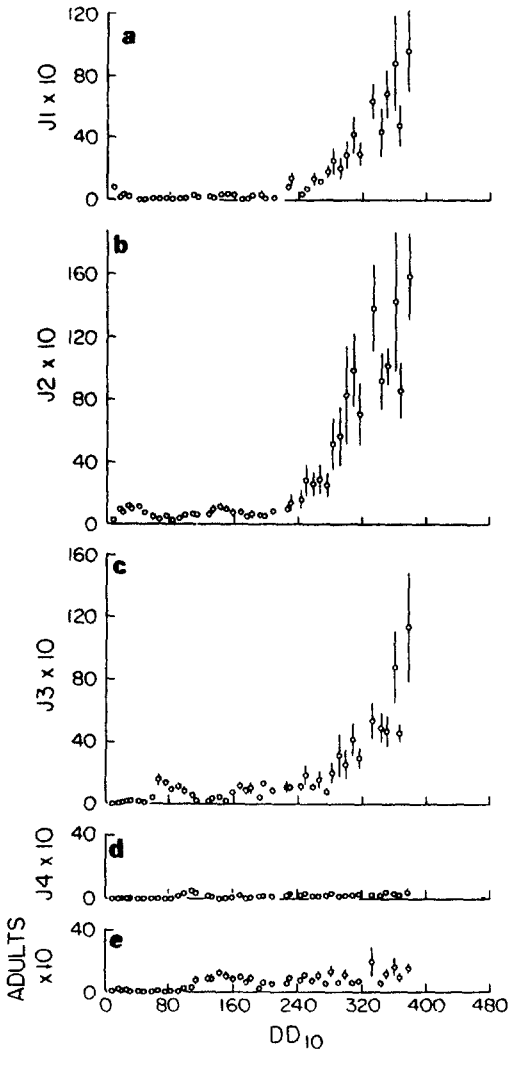

FIG. 4. Numbers of individuals of *Paratrichodorus minor* (whole data set) in each developmental stage over physiological time, assuming a basal threshold of 10 C. Points are the mean of 10 replications, bars represent the standard error of the mean. a) First-stage juvenile. b) Second-stage juvenile. c) Third-stage juvenile. d) Fourth-stage juvenile. e) Adult.

described by the linear regression equation (Fig. 5):

$$p(t) = 61.7 + 0.784t; \qquad r^2 = 0.965;$$

where p(t) is the total progeny at time t, and t is the time in DD_{10}. The slope of the line estimates the reproduction rate as 0.784 offspring/(female·DD_{10}^{-1}). Extending the line to the time axis estimates the first appearance of progeny at 79 DD_{10} after inoculation. The maximum length of

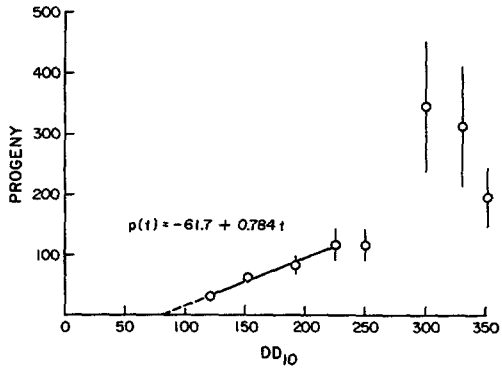

FIG. 5. Numbers of progeny from a single female of *Paratrichodorus minor* over physiological time. Vertical bars represent the standard error of the means. —— is the linear regression line fit to the first four points.

the fecundity period could not be determined because of the development of offspring females. The first newly gravid female appeared between 152 and 192 DD_{10}. When the pre-oviposition period of 79 DD_{10} was subtracted, a minimum length of reproduction was estimated as 73–113 DD_{10}. Total minimum egg production was then calculated as 57–86 eggs per female.

Presence or absence of host: The effective initial inoculum levels were 4 ± 5.7 J1, 13 ± 12.8 J2, 80 ± 36.0 J3, 32 ± 22.9 J4, and 14 ± 11.6 adults. Total populations in the presence of a host declined from the time of inoculation through 67 DD_{10}, then increased reaching a mean level of 379 nematodes after 300 DD_{10}, giving Pf/Pi = 2.6 (Fig. 6f). In the absence of a host, total populations declined by 67%. In the presence of a host, J1 numbers increased rapidly as eggs laid by the adults in the initial inoculum hatched, but in the absence of a host, there was no J1 increase (Fig. 6a); J2 followed the same patterns as the J1 (Fig. 6b). Both in the presence and absence of a host, J3 numbers declined initially (Fig. 6c), then increased in the presence of a host as the progeny of the adults reached J3 maturity. In the absence of a host, J3 numbers declined to 20% of the initial inoculum and remained at that level. The difference in the slopes of the initial population decline may reflect a decline due to maturing into the next stage in the

presence of a host and a decline due to mortality associated with the absence of a host. Numbers of J4 followed the J3 patterns: an initial decline with or without a host, although at different rates, followed by an increase in numbers in the presence of a host (Fig. 6d). Numbers of adults initially increased in both the presence and absence of a host, but not as much in the absence of a host (Fig. 6e). Following a decrease, the population of adults again increased in the presence of a host as the progeny of the initial adults reached maturity. The adult populations remained low in the absence of a host.

Discussion

This research was undertaken to obtain information necessary for the construction of a nematode population model. Egg hatch at 53.3 ± 7.3 DD_{10} agrees with earlier studies (2,3,10) and also provides a measure of the standard deviation. The close agreement between results using agar and soil suggests that for egg development, seedlings grown on agar plates are an adequate representation of the soil plus host-root-system environment.

Variation in the population counts, indicated by the standard error bars (Figs. 3, 4), consisted of inherent genetic variation among individuals compounded by destructive sampling procedures necessary in soil systems. The same individuals were not observed at each sampling period. The initial inoculum was not a single age cohort; instead it resulted from egg production of thousands of females over 4–5 days. Some J1 were more mature than others, but because eggs are laid singly in the soil, and each female contains only two mature eggs at a time (2), some compromise in cohort resolution was necessary to allow production of the required amount of inoculum. The presence of a few adults in the initial inoculum also contributed to the variability. The second peaks observed for J2 and J3 were probably the result of reproduction by the initial adults. The stage-specific extraction efficiency will vary, depending on the extraction procedure used, and

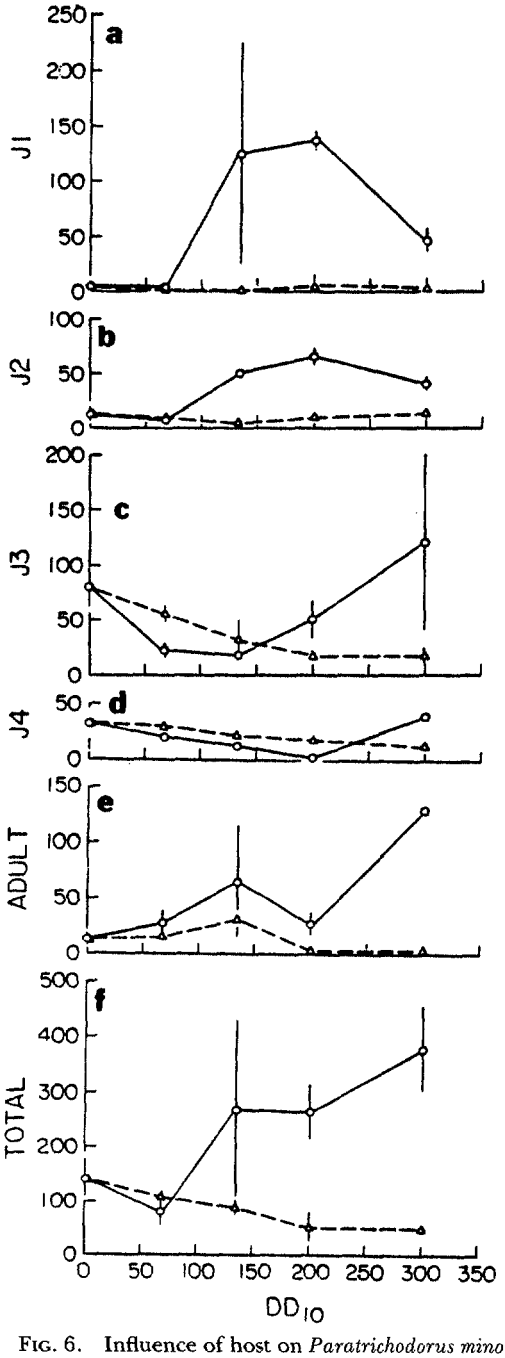

Fig. 6. Influence of host on *Paratrichodorus minor* populations over time. Points represent the mean of two replications and bars indicate the standard errors associated with these means. O——O host present, △——△ host absent. a) First-stage juvenile. b) Second-stage juvenile. c) Third-stage juvenile. d) Fourth-stage juvenile. e) Adult. f) Total population.

should be determined for each experiment. Error in the calculation or use of extraction efficiency correction factors may be a component of the variability in corrected population data.

Stage-frequency data resulting from the juvenile development experiment did not directly indicate the stage durations, standard deviations, and mortalities for each stage. Progression of the population from one stage to the next could be more clearly seen in first generation data (Fig. 3) than in the whole data set (Fig. 4). The stage duration and survivorship affected the total number of individuals present in a stage. The almost simultaneous increase in numbers of J1 and J2 and low numbers of J4 throughout the experiment were attributed to a very short J1 and J4 stage duration. These parameters were estimated from the stage-frequency database using analytical techniques reported elsewhere (15). The analysis resulted in a modification of the original conceptual model to include a pre-oviposition adult stage. Development of a database was necessary for the use of analytical methods to estimate the life cycle parameters required for a nematode model.

Reproduction of *P. minor* is density dependent, with the rate of population increase inversely related to initial population density (1,10). The fecundity study reported here used single gravid females to avoid a density influence and to circumvent the difficulty of determining how many females were producing progeny. Our observation of 117 offspring by 224 DD_{10} after inoculation of a single female onto sudan grass contrasts with the reported reproductive potential of *P. minor,* 12 progeny in 19 days at 29 C on Rutgers tomato (10). Differences in host suitability could contribute to this discrepancy (4). The use of an extraction efficiency correction factor in our experiments magnifies the difference in total numbers observed.

The fecundity rate estimated by the slope of the regression line (Fig. 5) was based on the total number of live progeny present at the time new gravid females appeared. Mortality sustained throughout the life cycle of the nematode population is embedded in the reproductive estimate. If an independent determination of stage-specific mortality could be made, the total population numbers could be adjusted. In the absence of these data, the actual population counts represented the best information available and were used to estimate a fecundity rate, realizing it probably underestimated the true value.

The beginning of reproduction was estimated as being the t-intercept of the regression line indicating a pre-oviposition period of 79 DD_{10}. The point at which the original female stopped egg production was masked by the reproduction of her offspring. Attempts to extract the female from the soil before any of the progeny became reproductive and to introduce the female onto a new plant failed.

In the absence of a host plant, 33% of the nematodes initially inoculated into soil were still alive after 300 DD_{10}, but no reproduction occurred during this time. These results agree with previous studies (11,13,17). Population of *P. minor* gradually declined in a sandy loam soil in the absence of a host from an initial population of 100 individuals, to a few individuals at 30 days, to no survivors at 60 days (13). Numbers of *Paratrichodorus anemones* Loof decreased from an initial population of 300 individuals, to 170 after 14 days (57% of the initial level), to 100 after 42 days (33% of the initial level), to no survivors after 168 days in a light sand soil and a loam soil in the absence of a host (17). Oocytes in females of *Trichodorus viruliferus* Hooper did not develop in the absence of a host, but in the presence of a host the oocytes developed rapidly (11).

Population studies of ectoparasitic nematodes are complicated by difficulty in obtaining a uniform age cohort, the necessity of using stage-specific extraction efficiencies to correct population counts, and the difficulty in determining fecundity rates without reliable estimates of stage-specific mortality. Parameterization of population models for plant parasitic nematodes is de-

pendent upon the development of techniques to address these problems.

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