A simulation model of soil nematode population dynamics: Effects of moisture and temperature

DARYL L. MOOREHEAD\(^1\), DIANA W. FRECKMAN\(^2\), JAMES F. REYNOLDS\(^3\)
and WALTER G. WHITFORD\(^3\)

With 8 figures

(Accepted: 87-03-01)

1. Introduction

We are currently constructing a simulation model of primary productivity, decomposition and nitrogen cycling in a Chihuahuan desert ecosystem (MOOREHEAD et al. 1987). This ecosystem simulation model will be used to address hypotheses concerning mechanisms of interactions and feedbacks which exist between the various organisms involved in carbon and nitrogen flow in deserts. The soil organism community is an important component of this model because of its recognized role in regulating numerous processes, e.g., nitrogen mineralization (SWIFT et al. 1979, ANDERSON et al. 1985). In this paper, we present a descriptive submodel of the population dynamics of a general bacterivorous nematode as influenced by soil temperature and moisture. Recent investigations suggest that nematodes may play an important role in regulating decomposition processes and nutrient cycling by grazing on microflora and microfauna (YEATES 1979, INGHAM et al. 1985).

Nematodes are aquatic animals, dependent on water availability for their activity. While most studies of nematodes have been in moist soils, e.g., woodlands and grasslands (ANDERSON et al. 1984, CLARHOLM et al. 1981, SOHLENUS 1979, SOHLENUS & BOSTRÖM 1986), nematodes are also abundant in arid and semi-arid ecosystems (SANTOS et al. 1981, FRECKMAN & MANKAU 1986). Nematodes respond to desiccation by entering an ametabolic, anhydrobiotic state, which is reversible with addition of moisture (DEMEURE & FRECKMAN 1981, FRECKMAN 1986). In the northern Chihuahuan desert, nematode activity has been shown to significantly affect litter decomposition rates (WHITFORD et al. 1983). Litterbags chemically treated to exclude nematode predators (microarthropods) had higher densities of nematodes and higher mass loss rates than those litterbags where nematodes were also excluded (SANTOS et al. 1981, 1984; WHITFORD et al. 1983, PARKER et al. 1984). PARKER et al. (1984) concluded that the elimination of microarthropods more closely coupled litter mass loss with nematode biomass and soil water content.

The influence of nematodes in nutrient cycling, as affected by abiotic factors such as temperature or decreasing soil moisture, remains unclear for deserts. Although specific data for nematodes in deserts are limited, our approach is to synthesize the available information into a working model that expresses the essential structure of the system regardless of whether or not the actual mathematical equations are exactly correct. In this case, modeling
serves as a valuable tool in the interplay between theory and experimentation. The objectives of this study are to summarize the available data, examine the relationships between nematodes and climatic variables, and to identify areas of additional data needs.

2. Model description

2.0. General remarks

Our modeling approach is similar to the microarthropod population model developed by Longstaff (1977) to examine age cohort dynamics. The concept of “physiological time” scales is used to adjust for the varying time requirements of nematode development at different temperatures, which has been carefully studied in arthropods (Stinner et al. 1974, van Straalen 1982, 1985a, b, Taylor 1981). Physiological time scales define physiological processes in terms of both temperature and time effects. For example, heat sums (degree-day values) are commonly used to measure development processes and Taylor (1981) defined a dimensionless development time scale (a cumulative index from 0 to 1), which accumulates through time at a rate determined by temperature-time relationships. In this model, we use a cumulative index similar to Taylor (1981).

The model has three components: eggs, larvae, and adults. No attempt was made to distinguish between larval stages or estimate larval development within the egg. Death, hatching and reproduction are driven by soil temperature, while soil moisture content determines the relative fractions of active and anhydrobiotic larval and adult populations. Daily age cohorts of eggs, larvae, and adults are followed through time until surviving eggs hatch, larvae mature and adults die, following Longstaff (1977) and the “stage-structure” approach described by van Straalen (1982). Physiological time scales are defined for egg and larva development.

Specific data concerning survival, fecundity, and development patterns were obtained from the published literature and laboratory experiments for a soil-dwelling, bacterivorous nematode genus, Acroboloides spp. This parthenogenic nematode was selected for this model since it is a common free-living soil nematode, is abundant in the Jornada creosotebush ecosystem on the northern Chihuahuan desert, and there are available data concerning many of its life history characteristics.

Table 1. Egg development time (EDT), generation time (GT) and total life span (TLS), in days, of several nematode species at various temperatures

<table>
<thead>
<tr>
<th>Temp. (°C)</th>
<th>EDT</th>
<th>GT</th>
<th>TLS</th>
<th>Species:</th>
<th>Reference:</th>
</tr>
</thead>
<tbody>
<tr>
<td>13</td>
<td>5.3</td>
<td>20.8</td>
<td>42</td>
<td>Acroboloides nanus</td>
<td>Sohlenius 1973</td>
</tr>
<tr>
<td>21</td>
<td>3.5</td>
<td>11.3</td>
<td>30</td>
<td>Plectus palustris</td>
<td>Schiemer et al. 1980</td>
</tr>
<tr>
<td>5</td>
<td>27.3</td>
<td>—</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>4.8</td>
<td>—</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>3.0</td>
<td>15.5</td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td>32.5</td>
<td>none</td>
<td></td>
<td>—</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>15.0</td>
<td>43.8</td>
<td>106.8</td>
<td>Monochoiodes potohikus</td>
<td>Yeates 1970</td>
</tr>
<tr>
<td>15</td>
<td>5.2</td>
<td>11.2</td>
<td>23.5</td>
<td>Mesorhabditis litoralis</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>2.7</td>
<td>8.3</td>
<td>33.8</td>
<td>Panaurolaimus australis</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>3.0</td>
<td>8.6</td>
<td>15.0</td>
<td>Panaurolaimus australis</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>3.0</td>
<td>9.0</td>
<td>11.8</td>
<td>Panaurolaimus australis</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>2.3</td>
<td>9.3</td>
<td>20.5</td>
<td>Acroboloides sylitis</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>2.8</td>
<td>8.8</td>
<td>23.5</td>
<td>Acroboloides sylitis</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>5.6</td>
<td>14.7</td>
<td>21.0</td>
<td>Zeldia punna</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>7.8</td>
<td>12.1</td>
<td>15.8</td>
<td>Zeldia punna</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>8.3</td>
<td>36.0</td>
<td>83.5</td>
<td>Acroboloides kolpogotonus</td>
<td></td>
</tr>
<tr>
<td>20</td>
<td>8.8</td>
<td>34.0</td>
<td>60.8</td>
<td>Acroboloides kolpogotonus</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>11.0</td>
<td>30.0</td>
<td>68.5</td>
<td>Monochius aquaticus</td>
<td>Jones 1977</td>
</tr>
<tr>
<td>20</td>
<td>12.5</td>
<td>26.3</td>
<td>56.3</td>
<td>Monochius aquaticus</td>
<td>Jones 1977</td>
</tr>
<tr>
<td>15</td>
<td>12.0</td>
<td>45.0</td>
<td>108.3</td>
<td>Monochius aquaticus</td>
<td>Jones 1977</td>
</tr>
<tr>
<td>22</td>
<td>4.9</td>
<td>20.0</td>
<td>52.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>4.0</td>
<td>16.1</td>
<td>43.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>28</td>
<td>3.6</td>
<td>14.1</td>
<td>36.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>5.7</td>
<td>32.0</td>
<td>—</td>
<td>Acroboloides complexus</td>
<td>Thomas 1965</td>
</tr>
<tr>
<td>20</td>
<td>3.0</td>
<td>15.5</td>
<td>&gt;65.5</td>
<td>Plectus palustris</td>
<td>Schiemer 1983</td>
</tr>
<tr>
<td>20</td>
<td>0.5</td>
<td>3.1</td>
<td>14.3</td>
<td>Caenorhabditis briggsae</td>
<td></td>
</tr>
</tbody>
</table>

362 Pedobiologia 30 (1987) 5
2.1. Development patterns

The relationships between temperature and development patterns in nematodes are well documented (Table 1); as temperature increases, egg development time (EDT), larval development time (LDT) and subsequent generation time (GT) decrease for a given species. *Acrobeloides* egg-to-egg GT versus temperature (Fig. 1) was described with a sigmoid equation based on laboratory culture data:

\[
GT = A + B \times \left[ C^2 / (C^2 + TEMP^2) \right]
\]

where TEMP is temperature (°C) and estimates for parameters A, B, and C are given in Table 2. Nematode cultures were developed from a sterile single egg transfer of an *Acrobeloides* spp. isolated from the soil in the northern Chihuahuan desert of southern New Mexico, U.S.A. Nematodes were maintained on a monoxyenic culture of *Escherichia coli*, and transferred weekly to assure nematode populations without dauer larvae.

The ratio EDT/GT varies little over temperature for a given species (Yeates 1970, Sohlenius 1973, Jones 1977, Greet 1978). Values of EDT and LDT were estimated for various temperatures (Fig. 1) based on calculated GT, assuming a linear relationship between EDT/GT and temperature (Sohlenius 1973):

\[
\frac{EDT}{GT} = D \times (TEMP) + E
\]

\[
LDT = GT - EDT
\]

where parameter estimates are given in Table 2.

The developmental stages of eggs (DEVP1) and larvae (DEVP2) at time (t) were estimated from prior development status at (t - 1) and EDT or LDT, respectively:

\[
DEVP1t = DEVP1(t-1) + 1/EDT_t
\]

\[
DEVP2t = DEVP2(t-1) + 1/LDT_t
\]

Developmental stages of freshly laid eggs or hatchlings were initialized at zero. When accumulated development reached 1.0, the eggs hatched or the larvae became adults.

2.2. Mortality

Egg and larva survival in various species of nematodes are affected by temperature. Both *Trichostylylus coloriformis* eggs and preinfective larvae have maximal survival at 4 °C, decreasing at temperatures above and below this optimum (Anderson et al. 1966). *Meloidogyne hapla* and *M. javanica* eggs show decreasing hatching success at temperatures above and below optima of 25 and 30 °C, respectively (Bird & Wallace 1965). Ferris (1976) found that both *M. arenaria* egg and larva death rates increased with increasing temperatures.

A parabolic relationship between egg hatching success and temperature (Bird & Wallace 1965, Ferris 1976) was used in this simulation with a maximum success (Succ) of 50% at 20 °C, and maximum (TMAX) and minimum (TMIN) temperature limits of 35 and 5 °C:

\[
Succ = 2 \times (TTemp - TMIN) \times (TMAX - TEM)/(TMAX - TMIN)^2
\]

Egg survival follows a negative exponential (Prosad 1959) or sigmoid (Anderson et al. 1966) curve. Therefore, an age-independent survival rate determined by development stage rather than chronological age was used:

\[
POP_t = POP_{t-1} \times Succ_{ADD}
\]

where ADD = 1/EDT.

Larva mortality data are not available for this genus. However, information from other groups show a sigmoid or negative exponential form of survival curve to be common (Prosad 1959, Anderson-
Fig. 1. Egg-to-egg generation time (GT), egg development time (EDT) and larva development time (LDT) as functions of temperature (°C).

Fig. 2. A. Adult-specific daily mortality rate as a function of age, and B. Resulting adult age-specific survival.

son et al. 1966, FERRIS 1976). Therefore, an equation similar to that of egg survivorship was used, assuming 50% survival to adulthood:

\[
\text{POP}_t = \text{POP}_{t-1} \times 0.5^{\text{ADD}}
\]

where ADD = 1/LDT.

Adult survivorship curves exhibit a variety of forms which are modified by interactions between temperature and food availability (SOHLENIUS 1973, ANDERSON & COLEMAN 1981, WOOMB & LAYBOURN-PARRY 1984). Longevity is usually presented as total life span (TLS) which sometimes includes time spent as a larva and, occasionally, time spent in the egg. Therefore, even though TLS decreases with increasing temperatures (Table 1), a large part of this is often due to decreasing development time requirements. Survivorship curves at various temperatures for *Rhabditis curviceudata, Paragigantelina berasienis* and *Diapigrasterillus nudicapsulatus* retain constant forms and comparable adult life spans although TLS varies (WOOMB & LAYBOURN-PARRY 1984). This pattern has also been observed in *Aeoboloides manus* (SOHLENIUS 1973).

Adult age-specific mortality (DX) was described by a sine function (Fig. 2a) of adult age (in days) and maximum observed mortality rate (DMAX) since total adult lifespan seems relatively independent of environmental conditions (SOHLENIUS 1973):

\[
\text{DX} = \text{DMAX} \times \sin(\text{AGE}/F \times \pi/2) \quad \text{if} \quad \text{AGE} \leq 17
\]

\[
\text{DX} = \text{DMAX} \quad \text{if} \quad \text{AGE} > 17
\]

The overall shape of the resulting adult survivorship curve (Fig. 2b) is similar to those of a number of other species (ANDERSON & COLEMAN 1981, WOOMB & LAYBOURN-PARRY 1984).

2.3. Fecundity

Decreasing temperatures increase the length of the reproductive period and decrease the daily reproductive rate. However, the total reproductive output (total number of offspring produced) in an individual life of *Rhabditis curviceudata, Paragigantelina berasienis* and *Diapigrasterillus nudicapsulatus* at various temperatures remains relatively constant (WOOMB & LAYBOURN-PARRY 1984).

Linear relationships were used to estimate both daily egg production per individual (RATE) and total number of reproductive days per individual (DAYS) as a function of temperature (SOHLENIUS 1973):

\[
\text{RATE} = 6 \times (\text{TEMP}) - H
\]

\[
\text{DAYS} = 1 - J \times (\text{TEMP})
\]

Laboratory studies show no other evident variation in age-specific fecundity for this group of nematodes (SOHLENIUS 1973).
2.4. Anhydrobiosis

Approximately 90—95\% of nematodes in a Mojave desert soil were estimated to be anhydrobiotic at soil moisture tensions of about —6.2 MPa (Freckman & Mankau 1986, Freckman et al. 1987) and the majority of nematodes in Chihuahuan desert surface litter and underlying soil have been observed to enter anhydrobiosis as the substrate dries (Whitford et al. 1981). Experimental work in the Chihuahuan system has shown that about 60\% of the nematodes become anhydrobiotic when soil water matric potentials reach approximately —0.4 MPa, corresponding to a soil water content of about 4.7\% (Freckman et al. 1987).

The active fraction of the nematode population (ACTIVE) was estimated by a sigmoid relationship between anhydrobiosis and soil moisture content (Fig. 3) (Freckman et al. 1987):

\[ \text{ACTIVE} = K^4 / [K^4 + (1 - H_2O)^4] \]  

where soil moisture (H\(_2\)O) is a fraction of water holding capacity. This equation assumes full activity at field capacity.

Only larvae and adults were considered to be affected by soil moisture content and these effects were limited to entering or exiting anhydrobiosis. Assumptions were made that: (1) all age groups of both larvae and adults responded identically to soil moisture conditions, (2) there was no larval development, adult aging or reproduction during anhydrobiosis, and (3) no mortality was associated with entering, leaving or existing in this state. Egg development was unaffected by moisture conditions, driven solely by temperature, with larvae capable of entering anhydrobiosis immediately upon hatching.

3. Simulations

The model uses a daily time step which is short enough to capture most of the dynamics of this system and yet still long enough to permit simulations of several days without requiring unreasonable computational time. To facilitate comparisons between simulations, the maximum number of active (nonanhydrobiotic) adults was standardized to 100 indi-
The adult population was not simply truncated at a particular age, but rather, the number of individuals in each age cohort was adjusted so that the overall age structure of the adult population remained proportional. Simulations were then run until egg, larva and adult populations were in dynamic equilibrium, i.e., the numbers of individuals in each group were equal on sequential days with identical environmental conditions; this equilibrium was achieved within 300 d in all simulations.

Temperature and moisture conditions used to drive the model lie within the summer extremes experienced in this environment. Frequent summer rainfall events and warm temperatures combine to produce the most favorable, albeit sporadic and brief, conditions for nematode activity. In order to examine both independent and combined effects of soil moisture and temperature on model behavior, five combinations of soil moisture and temperature regimes were used to drive the model.

3.1. Case 1

In our first simulations, the temperature was set at a constant 20, 25 or 30 °C and soil moisture at full water holding capacity. This was done in order to compare population dynamics at different temperatures when soil moisture was not limiting. Increasing the temperatures decreased the total numbers of eggs and larvae at equilibrium and also decreased the number of daily age cohorts in both populations (Fig. 4). This was the direct result of decreasing egg development time (EDT), hatching success (SUCC), and larva development time (LDT) with increasing temperatures. For example, EDT was 4.7 d at 20 °C, (producing five daily age cohorts) dropping to 1.9 d at 30 °C (Fig. 4a). This represents a 60% reduction in EDT, which reduced the number of daily age cohorts, increased population turnover rate, and led to fewer total numbers of eggs at equilibrium. In addition, hatching success (SUCC) decreased 44% (from 0.50 to 0.28) at the same time, resulting in greater daily egg mortality. This combination of factors led to reduced numbers of daily age cohorts and lower total populations of eggs at the higher temperature.

The decrease in egg hatching success reduced the daily input of youngest larvae (Fig. 4b) from 20 to 30 °C. Larva development time decreased 70% (from 10.8 to 3.2 d) at the same time. With fewer individuals entering the larval population and higher turnover rate, the standing population was much smaller at the higher temperature.

The daily egg production rate actually increased with increasing temperatures (597 eggs d⁻¹ at 20 °C and 982 eggs d⁻¹ at 30 °C) resulting in larger populations of the youngest egg cohort at higher temperatures (Fig. 4a). However, this 64% increase in egg production was insufficient to compensate for the decreases in EDT, SUCC and LDT, and a net reduction in the equilibrium numbers of eggs and larvae resulted.

3.2. Case 2

For this simulation, temperature was set at 20 °C, raised 1 °C d⁻¹ for 10 days and then lowered 1 °C d⁻¹ for 10 days (Fig. 5c), in a cyclical fashion, while maintaining soil moisture at constant full water holding capacity. This was done to examine the effects of gradual temperature fluctuation on nematode populations when soil moisture was optimal. As temperatures increased, the daily egg production rate increased but the total number of accumulated eggs diminished (Fig. 5a), for reasons explained above. The saw-toothed nature of the curve was the result of using a daily iteration rate which reflected changes in development time in whole-day increments, e.g., EDT was 4.3 days at 21 °C with eggs hatching on day 5 while at 22 °C EDT was 3.9 days and hatching occurred on day 4. This resulted in a sharp discontinuity in the egg population curve between these temperatures (Fig. 5a).

The numbers of larvae in the youngest daily age cohort also fluctuated greatly between certain temperatures, since this population was driven by the hatching of eggs (Fig. 5b). For example, as temperatures increased from 24 to 25 °C a one day decrease in EDT resulted in an extra surge of hatching. Conversely, when temperatures were decreasing, this same 1 °C change produced a one day increase in EDT, resulting in a day of no hatching.
Fig. 5. Effects of fluctuating temperature at constant optimum soil moisture content: A. Eggs laid (lower line) and existing eggs (upper line), B. Hatchlings (lower line) and existing larvae (upper line), and C. daily temperature.

Fig. 6. Effects of soil moisture content (percent water holding capacity) on equilibrium populations of active and anhydrobiotic individuals: A. Adults, and B. Larvae.

Gradually modifying the temperature over time illustrated an interactive relationship between egg and larva populations (Fig. 5a, b). Development times were minimized as temperatures increased, contributing to low standing populations since turnover was rapid. As temperatures decreased, EDT and egg survival increased, resulting in the rapid accumulation of a large population of eggs. Larva populations began to rapidly increase a few days following the rise in egg populations when increasing numbers of accumulated eggs began to hatch and increasing LDT further led to the accumulation of larvae. Overall, total larva populations increased as temperatures dropped (Fig. 5b) while the number of hatchlings rose slightly but inconsistently.

3.3. Case 3

In this case, the temperature was set a constant 25 °C and soil moisture content was set a constant 100, 50 or 25% of full water holding capacity. This was done in order to compare the effects of various levels of anhydrobiosis (determined by soil moisture content) on population dynamics.

The results showed large differences in the anhydrobiotic proportions of both larva and adult populations (Fig. 6). Anhydrobiotes accumulated at low soil moisture content, greatly exceeding the active population, as the result of several interacting factors: (1) the constant production and development of eggs, (2) the constant production and development of larvae, and (3) the maintenance of a constant active: anhydrobiote ratio for both larvae and adult populations.
First of all, egg production was not directly affected by soil moisture content and therefore remained constant (798 eggs d⁻¹) between simulations, since an active population of 100 adults was maintained at all soil moisture levels. Secondly, neither egg development nor hatching success were affected by soil moisture. The constant production, development, and hatching of eggs led to the constant production of hatching larvae.

An active fraction of each nematode cohort (adults and larvae) was maintained at the given soil moisture level (described previously). The ratio of active: anhydrobiotic individuals was maintained by activating anhydrobiotes as active individuals died or anhydrobiotes accumulated, and by placing the appropriate numbers of newcomers to each age cohort (larvae and adults) in anhydrobiosis.

The continuous production, development, and hatching of eggs provided a constant input of hatching larvae, which were divided into the required active and anhydrobiotic fractions. The active individuals developed or died while the anhydrobiotes did neither, leading to an
initial accumulation of hatchling anhydrobiotes. Since the model maintained a constant ratio of total active: anhydrobiotic hatchlings, additional numbers of anhydrobiotes were subsequently activated to satisfy this requirement. This increased the number of hatchlings maturing, leading to an initial increase in the number of larvae entering the next age class, and so the cycle continued. This is the mechanism which drove the accumulation of anhydrobiotic individuals at all ages (adults and larvae).

The total potential for the accumulation of anhydrobiotes was determined by maintaining both the active: anhydrobiote ratio and a population of 100 active adults. Since the production, development, and mortality functions were unaffected by soil moisture content, and the maximum number of active adults was constant, the equilibrium numbers of active adults and larvae also remained constant for all simulations. The only thing that changed was the size of the anhydrobiotic population at equilibrium, which was determined by the ratio of active: anhydrobiotic individuals. The reason that the anhydrobiotic component of the adult population exceeded that of the larvae was because of the additional removal of active adults in excess of the 100 individuals maintained by the model.

3.4. Case 4

For this simulation, temperature was set at a constant 25 °C while soil moisture content was set at full water holding capacity every 10 days and diminished during the intervals as a negative exponential function of time with a half-life of 2 d. This scenario represents a more realistic soil moisture regime for the desert. Figure 7 presents a 12-day segment from the model output, illustrating the response of the population to soil wetting and drying cycles. Soil moisture content peaked on days 2 and 12 of this time span and was at its lowest level on days 1 and 11 (Fig. 7a). The active fraction of the nematode population also followed this pattern (Fig. 7a).

Daily egg production varied little, remaining between 775 and 800 eggs d⁻¹ due to the limit of 100 active adults. The small fluctuation that did occur was because this 10-day moisture cycle caused shifts in the age structure of the adult population and the younger individuals have a higher reproductive potential. The large drop in the number of newly matured adults occurring on day 8 of the simulation segment (Fig. 7b) was followed by a drop in egg production, since without the high input of young individuals the adult population came to consist of older individuals.

Relatively large numbers of anhydrobiotic larvae accumulated in all age cohorts during the dry period (see Case 3), all of which became active when soil moisture reached full water holding capacity (Fig. 7d). The activated anhydrobiotes began to experience mortality, which led to a reduction in the total number of larvae (Fig. 7d). Since it took 7 d for larvae to develop into adults, the last of these activated anhydrobiotes had become adults on day 7, resulting in the observed decline in the numbers of newly developed adults on day 8 (Fig. 7b). Total adult populations stabilized at this point (Fig. 7c) because the number of larvae maturing during the next 3 d was limited by the activity ratio, and insufficient time to force additional larvae through the development process as a result of accumulating anhydrobiotes in all larva age cohorts (see Case 3).

3.5. Case 5

In the final simulation, temperature was set at 20 °C, raised 0.5 °C d⁻¹ for 20 d and then lowered 0.5 °C d⁻¹ for 20 d, in a cyclical fashion, while soil moisture was set at field capacity every 10 d and diminished during the intervals as a negative exponential function of time with a half-life of 2 d. This combined fluctuating temperature (Fig. 8c) and soil moisture (Fig. 8d) regimes in order to examine their combined effects on population dynamics. Figure 8 illustrates a 60-day segment of this simulation.

Jointly fluctuating the soil temperature and moisture regimes produced highly variable populations of eggs (Fig. 8a) and larvae (Fig. 8a, b), combining patterns observed in prior simulations (Cases 2 and 3). Part of the curve irregularities were again due to the model
iteration step representing whole-day changes in development times, especially evident in total egg and hatching populations (Fig. 8a).

Patterns of population dynamics primarily determined by temperature-dependent relationships remained little affected by soil moisture fluctuations. Egg production rates and the number of old eggs (at least one day old) over time varied as a function of temperature (Fig. 8a). In addition, the number of hatchlings remained essentially constant over time (Fig. 8a). All of these results were consistent with prior observations.

The patterns in active and total larva populations (individuals at least one day old) showed more variability (Fig. 8b). Irregularities in the pattern of total larva population over time were due to both changing temperature and soil moisture regimes. Sharp decreases in the total population corresponded to hatching delays (due to temperature changes) and increased mortality associated with the activation of anhydrobiotes (Fig. 8a, b), discussed under Cases 2 and 4. However, the interaction of soil moisture and temperature regimes resulted in a shift of peak total population values from a time of increasing temperature (Fig. 5b) to a time of decreasing temperatures (Fig. 8b). This response resulted, primarily, from the effects of soil moisture content on activity patterns.

The peak numbers of active larvae were also determined by temperature although short term activity patterns showed a much greater effect of soil moisture content (Fig. 8b, c, d). However, these soil moisture effects were not independent of temperature since the variation in activity level was greater at higher temperatures (Fig. 8b). This interaction had 2 major components: (1) shorter development times at higher temperatures permitted a more rapid population growth during favorable soil moisture conditions, and (2) the protection of anhydrobiotic individuals from mortality at low soil moisture conditions permitted large accumulations of anhydrobiotic individuals. Therefore, maximum total population and activity potentials resulted from greater population growth at higher temperatures and the accumulation of large numbers of anhydrobiotic individuals, protected from mortality at low soil moisture.

4. Summary

This study illustrates the potential importance of soil moisture and temperature effects on the population dynamics of soil-dwelling nematodes. The interaction of temperature and moisture responses ultimately controls activity patterns and potential population levels in this model. Nematodes survive limiting moisture conditions by entering anhydrobiosis, which helps to maintain potentially large, readily activated populations, as long as the temperature is favorable. This may be of major importance in the northern Chihuahuan desert where most rainfall occurs during relatively low input, frequent convection storms in the warmer summer months. Most organic materials and nematodes are in the surface soil layers in this ecosystem (Whitford et al. 1983), which dry quickly during the summer. Nematodes are apparently decoupled from nutrient cycling processes during dry periods so rainfall frequency may have an important effect on the decomposition processes influenced by nematode activity, as suggested by Parker et al. (1984).

Although there has been considerable field work on the interaction of soil fauna, rainfall quantity, and decomposition in deserts (e.g., Whitford et al. 1981, 1983, 1986; Steinberger et al. 1984, Parker et al. 1984), these data are insufficient for direct model validation. However, long term observations indicate that nematode populations in the field remain relatively constant through time, in spite of frequent intervals of unfavorable soil moisture conditions (Freeman et al. 1986). Our model suggests that anhydrobiosis, coupled with high reproduction and rapid development rates during the summer, may be an important mechanism for maintaining these populations.

Additional information is needed for further model development. For example, higher mortality rates occur in desert soils than in the monoxenic nematode cultures used as a basis for this model. Schneider (1985) noted that the mortality rates of a plant feeding nematode, Panagrolaimus minor, in the field greatly exceeded those of the nematode in greenhouse culture studies. Predation is probably a major cause of natural mortality but has not been quantified in situ.

There are also factors which are known to affect nematode population dynamics, but would be difficult to include in model formulation. For example, Schiemer (1983) found that the quantity and quality of available food had significant effects on the development and life span of free-living soil nematodes in laboratory cultures. Similarly, Noling & Fenn (1986) noted that reproductive rates of a plant-feeding nematode, Meloidogyne hapla, varied with population density and food supply. However, no information on food resources is available for this desert ecosystem.

Studies of the complex interactions occurring in ecosystems are increasingly aided by computer simulation models. Benefits of using these models include the recognition of information gaps and
previously unknown interactions. Our model is a useful tool for further research in soil biotic interactions and identifying areas of needed study. Certainly, construction of this model has identified research efforts to be directed towards obtaining additional information on nematode activity. Specifically, this would include quantification of: (1) short term responses of desert soil nematode populations to rapid soil moisture fluctuation, and (2) survival characteristics (eggs, larva and adults) under normal conditions of temperature, moisture, food availability, and predation.

5. Acknowledgements

We thank Dr. S. M. Schneider, USDA, and North Carolina State University for her helpful comments. The construction of this model was supported by NSF grant BSR-8507380, with field support by NSF grants BSR-821539, BSR-814466, and BSR-821557.

6. References


Clarholm, M., B. Popovic, T. Rosswall, B. Soderstrom, B. Sohlenius, H. Staaf & A. Wiker, 1981. Biological aspects of nitrogen mineralization in humus from a pine forest podsol incubated under different moisture and temperature conditions. Oikos 37, 137–145.


Straalen, N. M. van, 1983. Demographic analysis of arthropod populations using a continuous stage-variable. J. animal Ecol. 51, 769–783.


Address of the corresponding author: DARYL L. MOOREHEAD, Systems Ecology Research Group, San Diego State University, San Diego, California 92192, U.S.A.

**Synopsis:** *Original scientific paper*


A model of nematode (Acrebeloides spp.) population dynamics was used to examine the activity patterns of free-living nematodes in the northern Chihuahuan desert, New Mexico, U.S.A. A range of soil moisture and temperature conditions characteristic of this site were used to drive the model. Nematodes enter a cryptobiotic state (anhydrobiosis) when soil moisture is limiting, a condition which is quietly reversible when adequate moisture becomes available. Therefore, anhydrobiotes persist during dry periods, insuring the immediate activity of a nematode population following rainfall. Eggs and larvae develop quickly at warm summer temperatures, providing a high potential growth rate for the population when moisture is not limiting. Most annual precipitation in the northern Chihuahuan desert falls in frequent summer convection storms when temperatures are high and soils dry quickly. Model results suggest that rainfall frequency is a major determinant of nematode activity patterns in surface and shallow soil layers. Predicted activity patterns were consistent with field observations of nematode-related decomposition processes.

**Key words:** Desert, ecosystem, nematodes, soil fauna, population model.