Nematode Temperature Responses: A Niche Dimension in Populations of Bacterial-feeding Nematodes[1]

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Abstract: The optimum temperatures for population development were determined for six species of bacterial-feeding nematodes from among eight temperatures, ranging from 5 to 40 C. Four of the species are cohabiting species. The range of temperatures over which population development occurs (temperature niche breadth) is different for the cohabiting species. This difference may be a means of reducing competition between species, thus increasing temperatures over which habitats can be exploited. *Key words: bacterial feeding, nematodes, temperature response.*

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Soil nematode communities usually are much more diverse than those of other soil mesofauna (22,38,40,41), indicating that cohabiting species of nematodes must occupy different niches by partitioning resources (*niche dimensions*) between species and within trophic groups or through different tolerances of environmental conditions (niche breadths).

The ecological niche of an organism is both the space occupied by the organism and its functional role in the community. Thus, there are spatial, trophic, habitat, and other aspects of the niche. The niche is defined by all of the different factors (niche dimensions) affecting the organism. The niche is multidimensional in space and time. Thus, the complexity of the nematode community depends on the number of niche dimensions and differences in niche breadths between cohabiting species. The most obvious niche dimension is food source. Nematodes occupy almost every trophic level, from primary consumer to higher order predator (34). Another niche dimension, soil texture, affects nematode movement and size and the availability of prey (2,8, 37,40). Moisture, a third dimension, is closely linked to texture and temperature but also directly affects anabiotic responses of nematodes (26,30,34). Other niche dimensions are pH and the oxygen and organic matter content of the soil. Because the niche is n-dimensional (16), evaluating niche hypervolume at a resolution sufficient to observe responses of species is difficult. However, dimensions with easily observed mechanisms for species coexistence may be examined. Temperature is such a dimension because it can easily be regulated.

Nematodes are subjected to a wide range of temperatures. Temperatures near the soil surface may fluctuate greatly, both daily and, in the top 20 cm, by as much as 20–30 C seasonally. Various nematode responses to temperature have been investigated (reviewed in 21,23). Temperature has been shown to affect rate of development (5,6,14, 15,24,31,39), generation time (9,15,24), egg production and hatching (4,5,9,10,14,18,24, 25,29,31,33,35,39; also see Table 1 in 29 for optimum hatching temperatures of plant-parasitic nematodes), sex ratio (9,10,11,13, 17,20), size (9,19), chemical tactile responses (7), movement (7,27), respiration (1,18,28), and infectivity (12,26,36). The effect of temperature on these responses varies. For example, generation time may be shortened and survival of eggs and larvae may be greatly reduced at high temperatures (usually greater than 30 C), but more males may be produced. Consequently, even though generation time is shorter, the size of the developing population may be smaller. Thus, the population response may be the most suitable measure of optimum temperature because it reflects the summation of several processes affected by temperature. We examined population densities and rates of population growth to determine the optimum temperature ranges for population development for six nematode species, then compared the overlap of the optimum temperatures of cohabiting species. Our primary hypothesis was that cohabiting species have different optimum temperatures for

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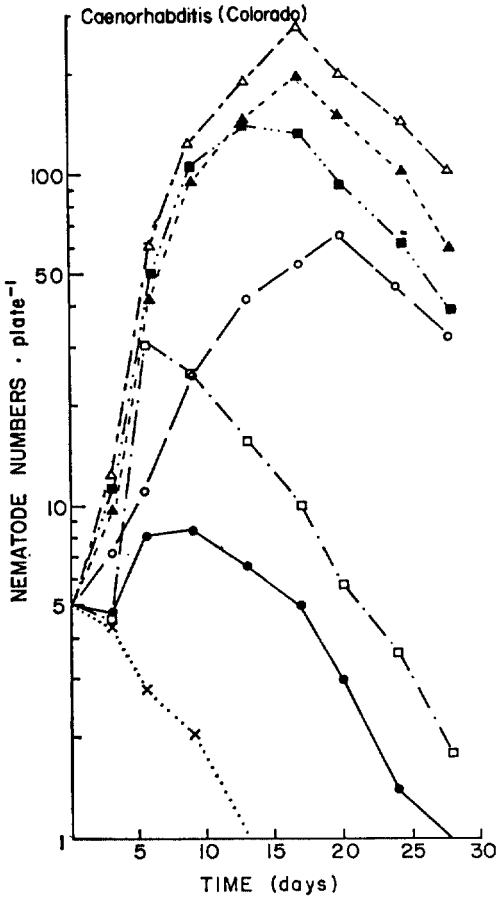


Fig. 1. Population development, including adults, juveniles, and eggs, at seven temperatures in *Caenorhabditis* sp. isolated from a shortgrass prairie in Colorado. The initial inocula consisted of five gravid adults for each temperature. Mean of five replicates.

5 C
10 C
15 C
20 C
24 C
30 C
35 C

maximum and most rapid population development.

MATERIALS AND METHODS

Six bacterial-feeding nematode species were isolated from three habitats. Four of the species (*Mesodiplogaster lheritieri*,

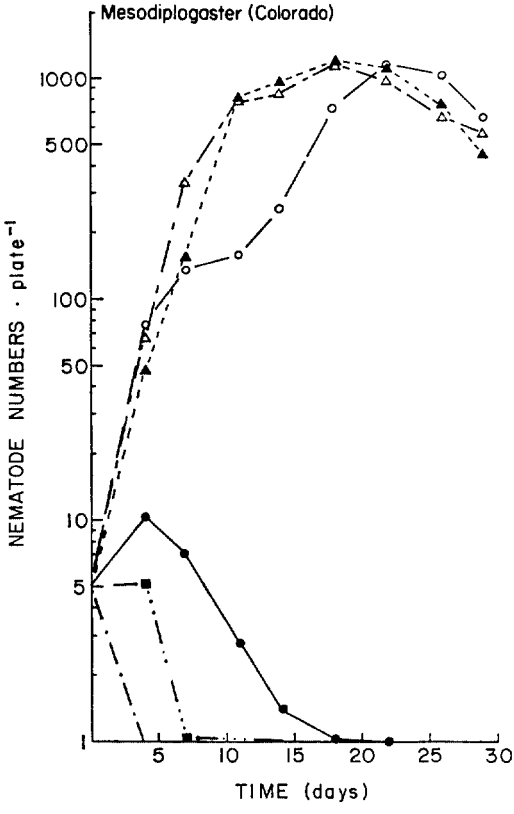


Fig. 2. Population development, including adults, juveniles, and eggs, at seven temperatures in *Mesodiplogaster* sp. isolated from a shortgrass prairie in Colorado. (Initial inocula and legend—same as in Fig. 1.)

Acrobeloides sp., *Pelodera* sp., *Caenohabditis* sp.) were from a shortgrass prairie in northeastern Colorado, one species (*Pelodera* sp.) was from a midgrass prairie in south-central Montana, and one (*Rhabditis* sp.) was from revegetated spent oil shale plots in western Colorado. All isolates were started from single gravid females (2), and cultures were maintained on 1½% agar plates with *Pseudomonas cepacia* as the food source. Stock cultures of each nematode species were maintained at room temperature for not less than 10 wk prior to the experiments.

From stock cultures, five gravid females of each species were placed on each of forty 52-mm agar plates with *P. cepacia* as the food source. Five plates of each species were then incubated in darkness at eight temperatures—5, 10, 15, 20, 24, 30, 35, and 40 C. Each replicate for each temperature was kept in plastic sleeves to prevent excessive

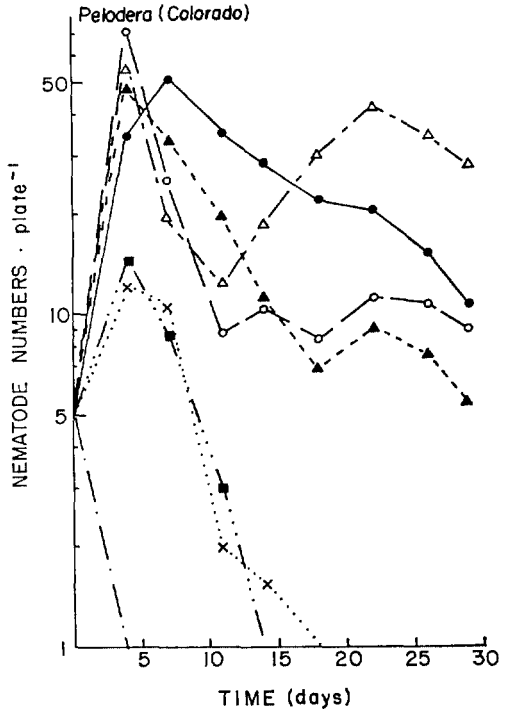


Fig. 3. Population development, including adults, juveniles, and eggs, at seven temperatures in *Pelodera* sp. isolated from a shortgrass prairie in Colorado. (Initial inocula and legend—same as in Fig. 1.)

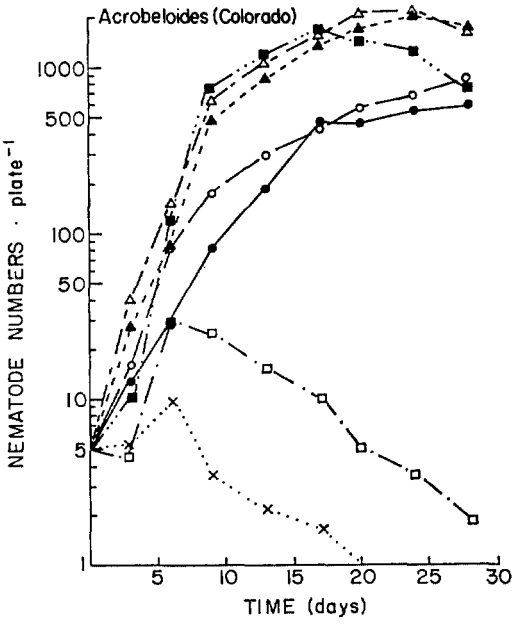


Fig. 4. Population development, including adults, juveniles, and eggs, at seven temperatures in *Acrobeloides* sp. isolated from a shortgrass prairie in Colorado. (Initial inocula and legend—same as in Fig. 1.)

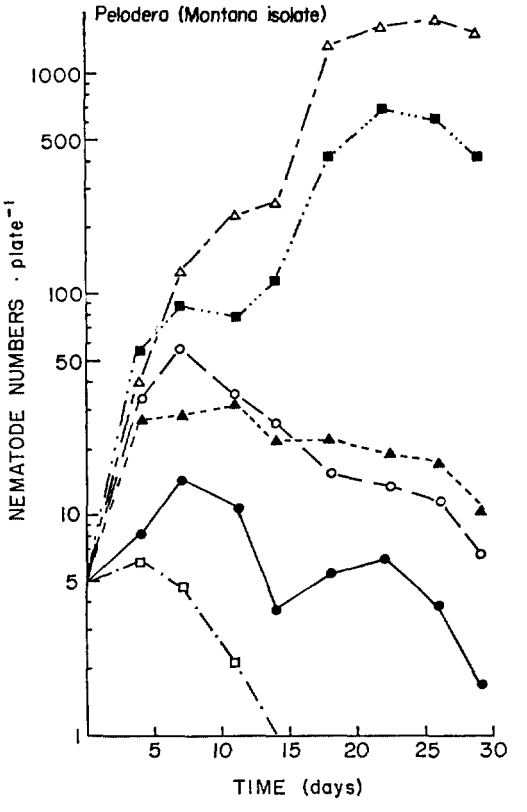
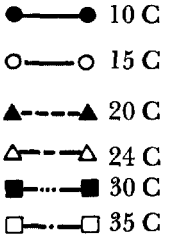


Fig. 5. Population development, including adults, juveniles, and eggs, at six temperatures in *Pelodera* sp. isolated from a midgrass prairie in Montana. (Initial inocula—same as in Fig. 1.)



water loss during the experiment. Direct counts of adults, juveniles, and eggs were made on each plate at 3–4-day intervals over a 29-day period.

RESULTS AND DISCUSSION

Population development for each species at each temperature followed one of three patterns (Figs. 1–6). The most common pattern (Figs. 1, 3, 5), an independent growth curve and significantly different population densities for each temperature, was found for the *Caenorhabditis* sp. and

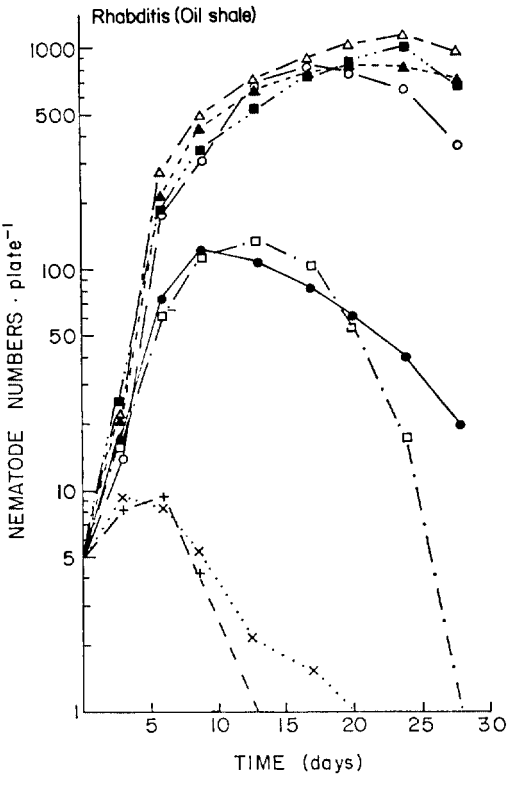


Fig. 6. Population development, including adults, juveniles, and eggs, at eight temperatures in *Rhabditis* sp. isolated from spent oil shale in Colorado. (Initial inocula—same as in Fig. 1.)

Pelodera sp. from the shortgrass prairie and the *Pelodera* sp. from the northern midgrass prairie. Population density was reduced at temperatures above or below an optimum 24 C for *Caenorhabditis* sp. and the northern *Pelodera* sp. and 15 C for the *Pelodera* sp. from the shortgrass prairie. This type of distinct temperature preference has also been reported for some species of tylenchorhynchids (19). Plotting the maximum population density at each temperature produces a slightly skewed bell-shaped curve (Fig. 7b, d). The range of temperatures under the mode of this curve is the niche breadth for temperature measured by maximum population production.

In the second type of pattern, represented by *Acrobeloides* sp. (Fig. 4) and *Rhabditis* sp. (Fig. 6), high population densities occur over a relatively wide range of temperatures. At 10 and 15 C in *Acrobeloides* sp. and 10 and 35 C in *Rhabditis* sp., maximum population densities were lower and/or population development was much slower than at other temperatures, and populations declined rapidly at these temperature extremes. Only the *Rhabditis* sp. population increased at 40 C; 10 individuals occurred after five days. The temperature niche breadth for both of these species is very wide (Fig. 7c), population development occurring over a temperature range of 15–20 C. The curve of maximum population density vs. temperature (Fig. 7c) for these two species reached a plateau, with a large area under the curve. In general, a wide range of temperature tolerance is not common, although the optimum generation time was over a 12-degree range for *Aphelenchoides besseyi* (15) and over an 11-degree range for *Diplolaimella ocellata* (14).

In the third pattern, produced only by *Mesodiplogaster* sp. (Fig. 2), populations developed at only a few temperatures, over a narrow temperature range, and when not increasing declined rapidly with no production of new individuals. Thus, the curve is much more narrow than that of the first pattern (Fig. 7a), and the area under the curve indicates that *Mesodiplogaster* sp. has a more narrow tolerance range than *Acrobeloides* sp. and *Rhabditis* sp. It should be noted that the species of *Mesodiplogaster* used in this study produce "dauer larvae" (3), which may be regarded as an adaptation to narrow tolerance. A narrow optimum temperature range is common for several nematode species (21,23), especially during the shortest generation time or period of maximum egg production, but a bell-shaped curve for population development is probably typical for most nematode species.

The amount of time required for population development is greatly affected by temperature (Fig. 8). Reaching maximum population density requires more time at

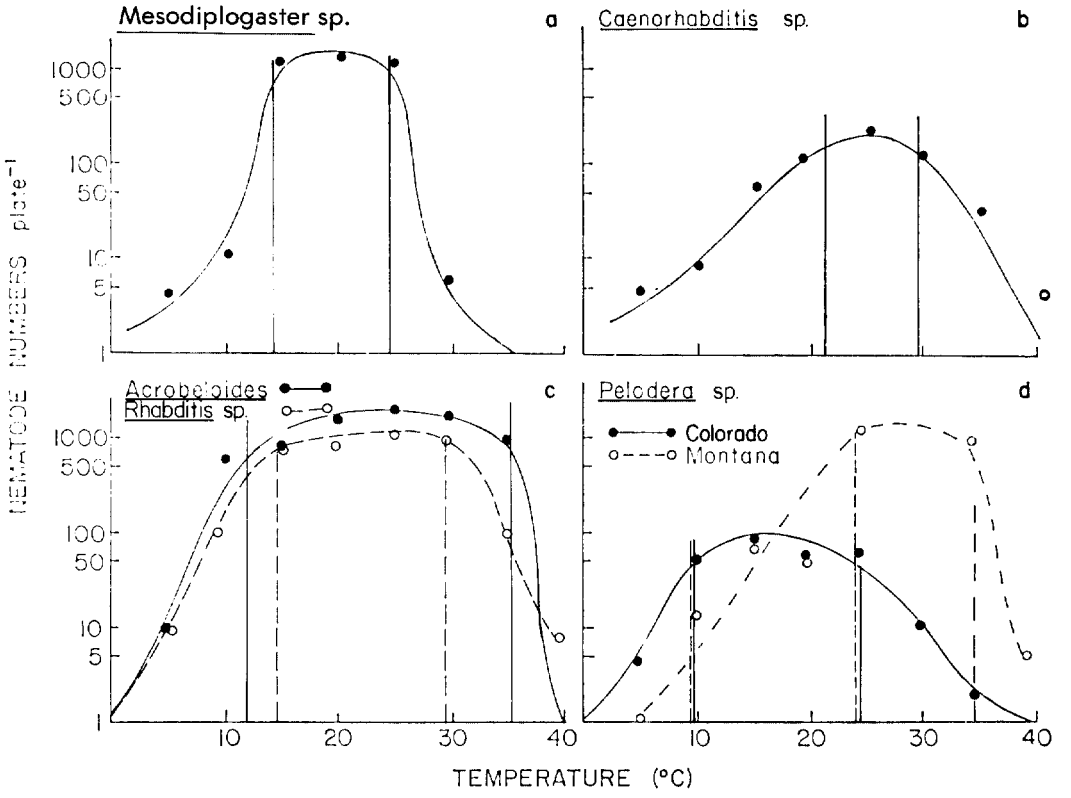


Fig. 7. Maximum population size (adults, eggs, and juveniles) for each species of nematode at each of eight temperatures: a) *Mesodiplogaster* sp. (Colorado), b) *Caenorhabditis* sp., c) *Rhabditis* sp. (oil shale), d) *Pelodera* sp. (Montana and Colorado). Vertical lines indicate mode of each curve.

low temperatures, 24 C or lower, than at temperatures above 24 C. Generation time is also directly related to temperature, but egg production is inversely related (6,9,11, 14,24). Both species that tolerated high temperatures, *Rhabditis* sp. and the Montana isolate of *Pelodera,* require more time to develop maximum populations at high temperature but less time at low temperature than the species from the shortgrass prairie. Because cold temperatures usually persist longer in the midgrass prairie and high plateaus of the oil shale region than on the eastern plains of Colorado, these species may have adapted to respond quickly, with rapid population development, at low temperatures. Tolerance of high temperatures may increase the period of productivity of the species, thus maximizing the length of activity in a comparatively short season. For the species from the shortgrass prairie, the longest period of maximum population development was between 10 and 15 C; above 15 C population decreased. Frequently, however, adults either died or did not reproduce at the extreme temperatures—5, 10, 35, or 40 C (Figs. 1–6); thus, the population density changed little. Adults at the extreme temperatures often survived for several days without laying viable eggs, a response reported for several other species (14).

As our primary hypothesis predicted, cohabiting species do have different temperature niche breadths (Fig. 9). Although optimum temperature ranges overlap, usually not more than three and frequently only two cohabiting species require the same specific optimum temperature. Thus, the difference in temperature optima may reduce competition between cohabiting species. *Acrobeloides* sp. has the greatest niche breadth but a longer generation time (11 days) than *Mesodiplogaster* sp., which has the narrowest niche breadth and a 4-day generation time (3). To compete successfully, a species with a long generation time may require a broader range of optimum

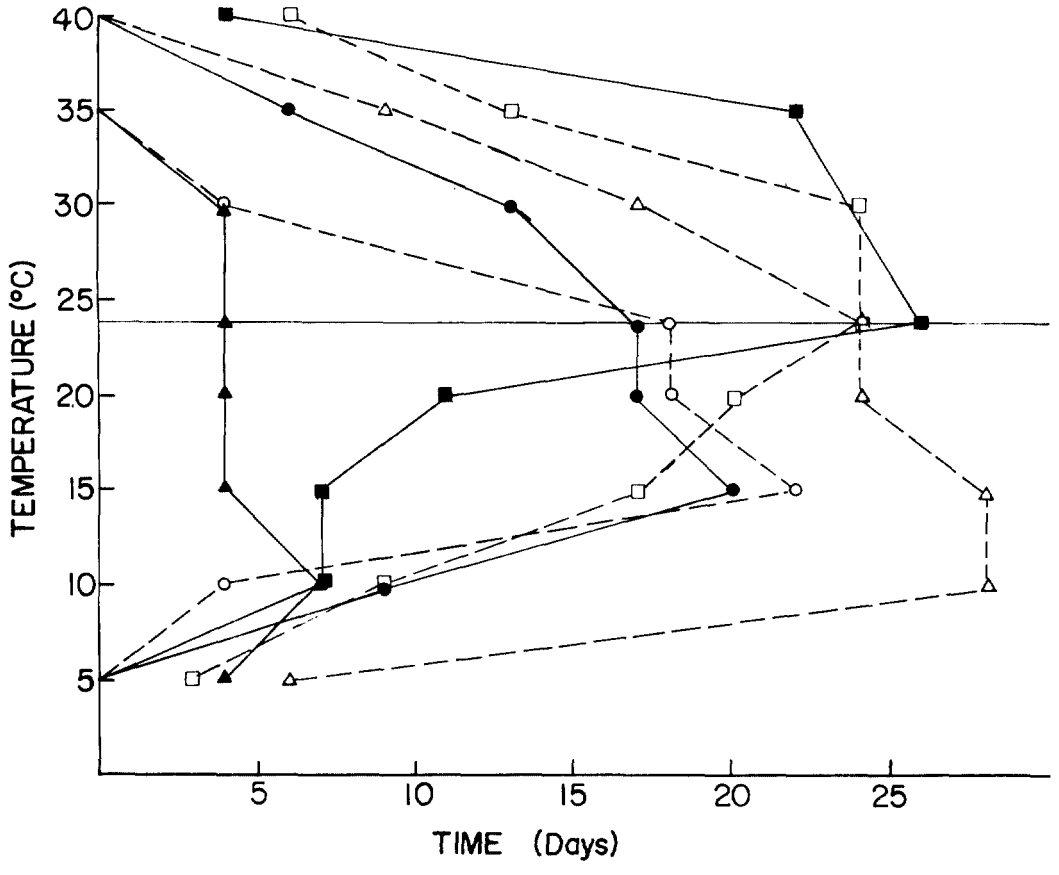


Fig. 8. Number of days required to produce the peak population for temperature and each species.

temperatures at which to remain active. This would provide a longer period of time during the year for the species to develop large enough populations to compete with species having a short generation time, particularly at temperatures where one species population development is reduced. The *Pelodera* species from the shortgrass prairie (Colorado) was active at colder temperatures than the *Pelodera* species from the midgrass prairie (Montana), perhaps because of selection resulting from the different temperatures in the habitats and different temperature requirements of the cohabiting species. Sudhaus (32) found that species collected from the tropics always had higher lethal temperature tolerances than sibling species from temperate regions.

In conclusion, some cohabiting species of nematodes have distinctly different optimum temperature ranges (niche breadths) for population development. This difference may be a means of reducing competition by preventing overlap of periods of population development. The width of the niche breadth may reflect the difference in the length of generation time in cohabiting species.

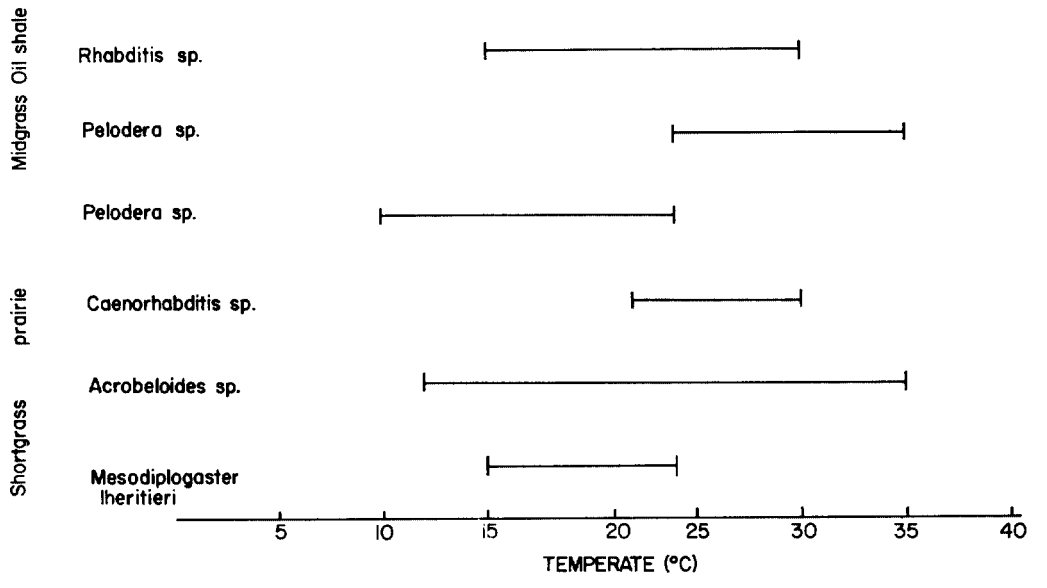


Fig. 9. Temperature niche breadth, based on temperature range over which sustained population development occurred, for each species of nematode.

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