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Effect of irrigation on nematode population dynamics and activity in desert soils*

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Summary. The nematode community in litter and soil was examined for a year in the Chihuahuan desert, before and after supplemental rainfall application. Proportions of nematode-active or anhydrobiotic forms and population densities were determined for 3 treatments: control (natural rainfall), a single, large (25-mm) monthly irrigation pulse, and 4 smaller (6-mm) irrigations spaced at weekly intervals. In litter the greatest nematode abundance was in the 6 mm week^{-1} treatment (48 nematodes 20 g^{-1} litter). Bacteriovores and fungivores accounted for approximately 95% of the numbers and biomass in all treatments. In soil, water amendments had no significant effect ($P < 0.05$) on annual mean densities of total nematodes, fungivores, bacterivores, or omnivore predators. Phytophage densities were greater on both irrigation treatments, with highest densities (9268 m^{-2}) in the 6 mm week^{-1} soils, which was 5.9% of the total soil nematode density. Total densities of individual trophic groups were not significantly different before or after rainfall. Soil nematode densities fluctuated independently with trophic group, month, and season. Bacterial feeders and omnivore predators were the largest contributor to total soil nematode density and biomass. Prior to irrigation, there were no differences in the percentage of anhydrobiotes on the three treatments. Anhydrobiotes decreased after irrigation in all treatments, and were significantly lower in soils of the larger, monthly irrigation. Nematodes were inactive (anhydrobiotic) and decoupled from decomposition processes when soil water matric potentials reached -0.4 MPa.

Key words: Nematode community – Chihuahan desert – Irrigation – Nematode extraction – Anhydrobiosis

Nematodes are ectothermic, aquatic animals and are confined to the water films surrounding soil particles. Their ability to survive desiccation in plant parts for 30-40 years and in soils for days to years at any stage of their life cycle has been the focus of many ecophysiological investigations (Demeure et al. 1979a, b; Freckman et al. 1980; Demeure and Freckman 1981; Freckman and Womersley 1983). Nematodes adapt to dehydration or freezing by entering into an inactive state termed anhydrobiosis or cryptobiosis, which is immediately reversible by reduction of the environmental stress.

Coventional wisdom holds that biological processes in deserts are regulated by rainfall (Noy-Meir 1973). Noy-Meir hypothesized that the pulse of biotic activity following rainfall would rapidly deplete the free energy compartment of organisms, leawing a small amount of energy held in reserve in the form of spores or anhydrobiotic or resistant stages. Previous studies in the Chihuahuan Desert have shown that 80 % of the nematodes in surface litter became anhydrobiotic 6 h after applying a simulated 25 mm rainfall, whereas nematodes in slower drying soil under the litter took 4 days to reach a similar level of anhydrobiosis (Whitford et al. 1981). While in anhydrobiosis the nematodes are essentially decoupled from the decomposition processes.

Studies of responses of desert soil nematodes to wetting and drying have been short term, i.e., 1 month or less (Whitford et al. 1981 ; Steinberger et al. 1984). We have no information on seasonal variation in short-term responses, nor information on the effects of

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varying levels of wetting and drying on the population dynamics of soil nematodes. As part of a year-long collaborative study of the effects of supplemental precipitation on decomposition processes (Whitford et al. 1985) and soil microflora and microfauna, we made a detailed study of the desert soil nematode community before and after water application for 1 year. We hypothesized that a single, large (25-mm) irrigation pulse should have a greater effect on decomposition, nematode densities, and nematode activity than four smaller (6-mm) irrigations spaced at weekly intervals. Both of these treatments should result in higher decomposition rates and more abundant soil fauna and microflora than a natural rainfall (Whitford et al. 1985).

Materials and Methods

These studies were conducted at the base of an alluvial plain in New Mexico at an elevation of 1000–2000 m. The soils are deep sandy loams with a calcium carbonate deposition layer (caliche) at approximately 70 cm depth. The dominant vegetation is a cover of cresote bush, *Larrea tridentata*, with scattered mesquite, *Prosopis glandulosa*, along drainage channels. The average annual rainfall is 211 ± 77 mm, with 70% of the precipation occurring in late summer. Summer maximum temperatures reach 40°C and winter temperatures regularly fall below 0°C.

The experimental design has been described in detail (Whitford et al. 1985) and is briefly described here. *L. tridentata* shrubs of approximately the same size were chosen: 70–100 cm in height and 100 cm canopy diameter. All leaf litter was cleared from under the canopy of the shrubs. Twenty-gram units of air-dried *L. tridentata* leaves were confined in aluminum window screen cylinders that were fastened to the soil surface under the shrub canopy. Rainfall amendments were provided by a sprinkler irrigation system situated at the ends of each 10 × 25 m plot that provided water above the plants. All plots received natural rainfall plus the following supplements: (1) control (no added water), (2) weekly applications of 6 mm water, and (3) monthly applications of 25 mm. There were three plots per treatment, with five replicates per treatment. The source of water for the irrigated plots was well water collected in a concrete holding pond. The water had an electrical conductivity of 0.8 mmhos.cm^{-3} with approximately 100 mg.l^{-1} NaHCO3 and NaCO3, and 200 mg.l^{-1} NaCl. Soil moisture tension was measured at 5 cm for each plot on each sampling date with Wescor soil psychrometers, and gravimetric soil moisture was determined from each soil sample. Soil moisture tension release curves and texture analyses were determined from soil collected at control plots. Soil temperatures were recorded for each treatment. Litter was carefully removed and soil cores (4.5 cm diameter and 10 cm deep) were collected immediately beneath the litter. Samples were removed from each plot between 0600 h and 0800 h, immediately before and 3 days after each simulated rainfall. Litter and soil cores were placed in plastic bags and shipped to the University of California, Riverside, for nematode extraction.

Litter extraction. Because most nematode extraction methods were developed for removing nematodes from soil, two methods, the mist chamber (Southey 1970) and a modification of the Coolen technique (Coolen 1979), were tested to determine the most efficient technique for extracting active nematodes from litter. *L. tridentata* leaf litter was weighed into 20-g aliquots and placed in 20 individual plastic bags. One milliliter of water containing 1000 ± 100 *Aphelenchus avenae*, a fungal feeding nematode, was sprayed into each bag, the bag sealed, and the nematodes and litter gently mixed. Litter from each bag was poured into a food processor and processed gently for 30 s. For the mist chamber method, litter from each of 10 bags was placed on the mist chamber and nematodes removed daily for 7 days.

Nematodes were extracted from the remaining ten bags using a modified Coolen technique, originally developed to extract nematodes from root fragments. This method consisted of the following: litter was blended with 200 ml water, poured into a centrifuge tube containing 2.5 ml kaolin powder, stirred for 30 s, and centrifuged at 1500 *g* for 4 min. Water was decanted, 1 *M* sucrose solution added to make a volume of 200 ml, the solution stirred for 30 s, centrifuged for 4 min at 1500 *g*, poured onto 5-μm Coolen sieves, and left for 5 min. The stoppers were removed from the sieves, the sieves sprayed with a fine water mist, and the nematode-water solution poured into a 150-ml beaker. Two drops of Separan (Dow Chemical Co) per beaker were added, and the solution was stirred, allowed to settle, and poured through a 500-mesh sieve.

The differences between the two techniques were significant ($P < 0.01$), with a mean recovery of 850 nematodes for the Coolen method and 420 for the 7-day total of the mist chamber. The nematodes in the samples included both bacterial feeding nematodes already present in the litter and the fungivore *A. avenae*. The mist chamber technique extracted a greater percentage of bacterial feeders, most of which were juveniles. Further replications of the Coolen technique with *A. avenae* indicated an extraction efficiency of 75%. Because the mist chamber extracted larger numbers of juveniles which may have hatched from eggs over the 7-day period, and because the fungivorous trophic group was not well represented by this method, the Coolen technique was used to extract nematodes from litter. All densities reported are corrected for extraction efficiency, and were calculated on the basis of numbers extracted from 20 g litter.

Soil extraction. Nematodes from soil samples were extracted by two techniques. To determine taxonomic identification, density and affiliation with trophic groups, one-half of the soil samples were processed by the modified sugar flotation technique (Freckman et al. 1975). The nematode genera and trophic groups were: bacterivores – *Acrobeles, Acrobeloides, Alaimus, Cephalobus, Panagrolaimus, Plectus, Rhabditida*; fungivores – *Aphelenchus avenae, Aphelenchoides, Ditylenchus, Stictylus*; omnivore predators – *Dorylaimus, Prismatolaimus, Pungentus*; plant feeders – *Quinsulcius, Paratylenchus, Tylenchorhynchus*. Nematode numbers were expressed as numbers m^{-2} at 0–10 cm depth, and were corrected for an extraction efficiency of 75% (Freckman et al. 1975). Bulk density of the soil (1.62 g/cm^3) was considered in calculations of the nematode density. Analysis of variance and studentized range test (Tukey's) were performed on the transformed (log $[X+1]$) numbers of nematodes.

Biomass was determined by measuring the lengths and widths of >100 nematodes per trophic group (Freckman 1982), and average individual weight per trophic group was calculated according to Andrassy (1956).

To assess the level of activity of the nematode population (anhydrobiotic or active) nematodes were extracted from the remaining soil by the anhydrobiotic technique (Freckman et al. 1977) and the percentage of coiled and straight nematodes determined. Coiled nematodes were considered indicative of the inactive, anhydrobiotic state (Demeure et al. 1979a).

Results and discussion

Litter nematodes

Only results based on the monthly analysis will be discussed here. Results of treatment effects on annual mean nematode and trophic group density in litter