Soil Biology & Biochemistry 40 (2008) 2366–2374

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

# Nematode community development early in ecological restoration: The role of organic amendments

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ARTICLE INFO

*Article history:*
Received 14 February 2008
Received in revised form 7 May 2008
Accepted 21 May 2008
Available online 20 June 2008

*Keywords:*
Remediation
Amendment
Mulch
Nematodes
Soil fauna
Mixed grass prairie
Texas

ABSTRACT

Soil food web structure is an integral component of ecosystem function, but there are few strategies orientated towards managing its development in restoration projects. The objective of this study was to direct nematode community structure and function through the application of organic amendments to the soil of an urban landfill remediation project using native grassland vegetation. We used a 2 × 3 factorial design in which an organic amendment was added to the soil at different locations (incorporated versus surface-applied) and amounts (none, light, heavy). Nematode and plant community structure were monitored over three growing seasons to determine the rate and direction of change. Surface application of organic amendments supported greater grass and total plant densities compared to incorporated amendment treatments, but plant density did not vary with amendment amount. Total nematode density, family diversity and family richness were not affected by the amendment treatments, but both family richness and seasonal nematode density increased over the duration of the experiment. Other descriptors of nematode community development (Structure, Maturity, and Plant Parasite Indexes) were not influenced by either amendment amount or location, but varied significantly over time. Contrary to expectations, the surface amendment treatments significantly increased bacterivorous, plant parasitic, omnivorous and predator nematode densities, but had no influence on fungi/root-tip feeding nematodes. Also contrary to our hypotheses, the surface treatments had smaller Channel Index and greater Enrichment Index values relative to the incorporated treatments during the first 15 month of the experiment. We hypothesize that the surface amendments are indirectly affecting the structure of the nematode community by promoting greater plant density, thus increasing the concentration of high-quality organic matter (such as root exudates) in the soil. This promotes the development of a nematode community dominated by opportunistic groups that respond rapidly to increased resource availability. Future studies should aim to distinguish between the organic amendment's direct function as a potential food source for the soil biota versus their indirect role as an environmental variable, including their capability to alter the availability of plant-derived resources.

## 1. Introduction

There is increasing interest among restoration ecologists for the development of strategies that will stimulate biotic interactions and promote the internal control of ecosystem processes in restored systems (Whisenant, 1999; Hobbs and Harris, 2001). Soil organisms are essential to many of these processes, such as the regulation of soil nutrient cycling and availability (Reever Morghan and Seastedt, 1999; Blumenthal et al., 2003) and also contribute to the development of improved soil structure (Caravaca et al., 2006) and improved plant productivity and diversity (Wardle et al., 1999; Verschoor et al., 2002; De Deyn et al., 2003). Complex soil biotic communities offer greater redundancy in function and should, therefore, require fewer management inputs (Smith et al., 2003). Although the failure to consider belowground biota can reduce the probability of restoration success (Zink and Allen, 1998; Korb et al., 2004), there are currently few restoration strategies that directly target and manage the development of this group of organisms.

Soil organisms in severely disturbed areas can be limited by the lack of soil structure and organic energy sources (Whitford et al., 1989; Zink and Allen, 1998). The application of organic amendments to the soil alleviates these conditions by providing a carbon substrate for the soil microbial community, altering soil nutrient status, and creating pore networks that facilitate interaction (Nahar et al., 2006). Amendment addition also promotes vegetation development by improving conditions for plant establishment and

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doi:10.1016/j.soilbio.2008.05.017

growth. For example, amendments can protect the soil surface from erosive forces, retain soil moisture and moderate surface temperatures (Winkel et al., 1991; Chambers, 2000).

Studies in agro-ecosystems have demonstrated the location of the organic amendment within the soil profile, surface-applied or incorporated at depth, can affect the community structure of soil organisms and the rate of their activity (Holland and Coleman, 1987). Incorporation increases the surface area exposure of the amendments to the decomposer community, and therefore supports larger populations and can have a more immediate impact on soil nutrient status (Beare et al., 1992). This amendment location also increases the habitable pore space for soil fauna, which can increase nutrient mineralization (Elliott et al., 1980; Freckman and Baldwin, 1990). Finally, the incorporated material supports relatively larger populations of bacteria and bacterivorous organisms because they can respond rapidly to resource enrichment (Beare et al., 1992; Fu et al., 2000).

In contrast, organic amendments left on the soil surface, such as residue retention in no-till agro-ecosystems, are utilized more slowly by soil organisms (Beare et al., 1992), and generally promote decomposition through the fungal decomposition channel. The physical separation of the surface amendment and mineral soil favors fungi because these organisms can translocate materials via hyphae between the aboveground organic residues and the belowground soil environment (Frey et al., 1999). Population sizes of consumers of fungi, such as fungivorous nematodes, also increase when amendments are applied to the soil surface compared to those that are incorporated (Beare et al., 1992; Fu et al., 2000). A decomposition channel dominated by fungi and their consumers is often the target of restoration (Zink and Allen, 1998) because this mode of decomposition tends to be more conservative at nutrient cycling than one dominated by bacteria (Myrold, 1999; Bardgett et al., 2002; Smith et al., 2003).

Nematodes have been widely used as indicators of the development of the soil fauna community (Freckman and Ettema, 1993; Neher, 1999). They are the most numerous soil mesofauna and are found in all ecosystems (Ritz and Trudgill, 1999). Nematodes occupy all consumer trophic levels within the soil food web and, therefore, their community composition can lead to insights regarding the structure and function of the soil ecosystem (De Ruiter et al., 2005). Additionally, nematode populations react quickly to disturbance (Bongers, 1999) and can be used to differentiate the effects of management practices (Freckman and Ettema, 1993; Neher and Campbell, 1994); therefore, several indexes have been developed to assess the structure and function of the nematode community following environmental change (Bongers, 1990; Ferris et al., 2001). On a practical level, they are easy to extract from the soil, require very little specialized equipment, and identification to family is relatively easy (Coleman et al., 1999; Ritz and Trudgill, 1999).

Here, we compared the ability of organic amendments to direct the development of soil fauna during restoration of landfill cap to grassland. To do this, we monitored the rate and direction of change of the nematode community during the first three growing seasons after restoration initiation as an indicator of soil ecosystem development. We hypothesized that: (1) the addition of organic material would accelerate the development of soil community structure, creating greater density and diversity of soil nematodes in all trophic levels, and the magnitude of change would be proportional to the amount of material added; (2) the rate of response would be faster in plots where the material is incorporated, as this creates closer contact with the soil, and therefore more rapid decomposition; and (3) organic amendments incorporated into the soil would favor nematode communities that respond to resource enrichment, such as bacterivores, whereas amendments applied to the soil surface would result in the development of nematode communities dominated by conservative groups, such as fungivorous nematodes.

## 2. Methods

### 2.1. Study area

This study was conducted on a 21 ha portion of the Castle Drive Landfill in Garland, Dallas County, Texas (32°93′N, 96°58′W; elevation 165 m). This site lies within the Texas Blackland Prairie Ecoregion, which is dominated by tall- and mid-sized grasses with associated forbs (Diggs et al., 1999). The mean monthly low temperature (1 °C) occurs in January and the mean monthly high temperature (36 °C) is in July. The 30-year precipitation average is 999 mm and has a bimodal distribution, with rainfall peaks in May (134 mm) and October (116 mm). Annual precipitation was below average in 2003 (510 mm) and 2005 (474 mm). Although the total amount of precipitation was average during 2004, June and July of that year had above-normal precipitation (Fig. 1).

This portion of the landfill was closed in 2002. In accordance with regulations by the Texas Commission on Environmental Quality, the landfill was covered with a constructed clay cap, which is 45 cm thick, and is designed to be impermeable to water seepage into the municipal garbage below. Overlaying this cap is a 26–35 cm composite of unconsolidated subsoil from an adjacent area and is a growing medium for the vegetation cover. Properties of this material are provided in Table 1.

### 2.2. Restoration treatments and experimental design

This experiment had six treatments in a 2 × 3 factorial completely randomized design. There were two amendment location treatments: surface-applied and incorporated to 6 cm with a rototiller. Within these two treatments, there were three amounts of amendment added to the plot: no amendment, a light amendment treatment ($765\ \mathrm{g\,m^{-2}}$) and heavy amendment treatment ($1530\ \mathrm{g\,m^{-2}}$). Plots were 5 m × 5 m (25 $\mathrm{m^2}$) and were separated from each other with 2 m alley ways. In all, there were 30 plots with each of the six treatments occurring once within five replicate blocks, which were along a 5% northeast slope. The experimental area was disked three times to remove any previous vegetation before planting on March 12, 2003.

The amendment material was untreated urban wood waste from the City of Garland Castle Drive Wood Recycling Facility. This

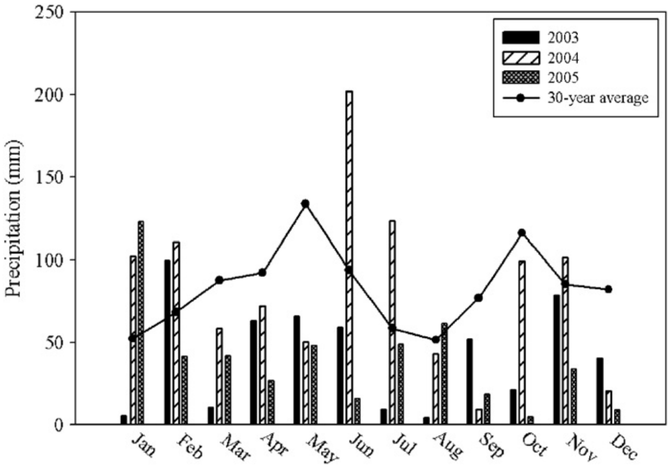

**Fig. 1.** Monthly precipitation data for 2003–2005 and the 30-year mean precipitation. Data are from the Rockwall, Texas weather station (National Weather Service) located approximately 8.5 km east of the Castle Drive Landfill, Garland, Texas.

**Table 1**
Initial soil characteristics (mean ± SE) of the experimental area at the Castle Drive Landfill, Garland, Texas, USA

| | Mean ± SE |
|---|---|
| Particle size distribution | |
| Sand (%) | 16 ± 2 |
| Silt (%) | 41 ± 4 |
| Clay (%) | 43 ± 2 |
| Bulk density (g cm$^{-3}$) | 1.45 ± 0.01 |
| pH | 8.2 |
| Soil organic carbon (g C kg$^{-1}$ soil) | 0.77 ± 0.05 |
| Soil total nitrogen (g N kg$^{-1}$ soil) | 0.058 ± 0.005 |
| Soil microbial biomass-carbon (g C kg$^{-1}$ soil) | 0.66 ± 0.03 |
| Calcium (mg kg$^{-1}$ soil) | 57,201 ± 73 |
| Magnesium (mg kg$^{-1}$ soil) | 476 ± 19 |
| Total phosphorous (mg kg$^{-1}$ soil) | 23 ± 5 |
| Potassium (mg kg$^{-1}$ soil) | 336 ± 3.8 |
| Salinity (mg kg$^{-1}$ soil) | 315 ± 32 |
| Sodium (mg kg$^{-1}$ soil) | 362 ± 16 |
| Sulfur (mg kg$^{-1}$ soil) | 56 ± 3 |

material had a composition of 43.5% carbon, 0.45% nitrogen and a C:N ratio of 98:1. Amendment particle size distribution was 26% of mass less than 1 cm$^2$, 17% greater than 1 cm$^2$ but less than 5 cm$^2$, and 56% larger than 5 cm$^2$. This amendment material was chosen primarily to ameliorate compaction and improve soil physical structure without creating a dramatic pulse of mineralization or immobilization (Whitford et al., 1989; Reid and Naeth, 2005).

Seeds of native and naturalized grasses and forb species were acquired from two commercial vendors: Turner Seed Company and Native American Seed. Planting technique varied slightly by location. For the surface application treatments, the large and awned seeds were hand-spread followed by the use of a culti-packer (Brillion Farm Equipment, Brillion, Wisconsin) to firm the seedbed. The amendment was hand-spread over the seedbed at the three treatment amounts. In the incorporated treatments, the large and awned seeds were hand-sewn, followed by the application of the amendment. The material was then incorporated to 6 cm with a roto-tiller and the seedbed firmed with the culti-packer. In both location treatments, the small seeded species were hand-sown after amendment manipulation. The total pure live seed applied was 2.1 g m$^{-2}$.

All unsown plants were enumerated along with the planted species. Except for the following three exceptions, unplanted species were not managed throughout the experiment. The abundant and large-leaved *Ambrosia trifida* L. (giant ragweed) and *Helianthus annuus* L. (annual sunflower) individuals were hand-clipped and removed from plots in June 2003 to minimize soil water loss during initial plant establishment. These species were untreated throughout the remainder of the experiment. *Sorghum halepense* (L.) Pers. (johnson grass), an aggressive invasive grass, was periodically treated throughout the experiment with individual wipe treatments of glyphosphate (*N*-phosphonomethyl glycine) herbicide.

### 2.3. Reference grasslands

The nematode communities of a native prairie and a restored grassland were also measured to compare with the landfill experiment. These two reference grasslands are located approximately 6.5 km southwest of the landfill site in Rosehill Park in Garland, Texas (32°86′N, 96°59′W). This park contains a 30 ha remnant of tallgrass prairie dominated by *Schizachyrium scoparium* Michx. (little bluestem) and *Sorghastrum avenaceum* Michx. (Indian grass). The urban prairie was acquired by the City of Garland in 1978 and has had no significant disturbance since that time (T. Frye, City of Garland Parks Department, personal communication), although there has been some encroachment by *Juniperus* L. species (juniper), *Rubus* L. species (dewberry), and *S. halepense*. Adjacent to the native prairie is a 28 ha area which was restored to prairie vegetation in the early 1990s. This area is currently dominated by an introduced C$_4$ grass, *Bothriochloa ischaemum* var. *songarica* Fisch. & Mey. (King Ranch bluestem), with infrequent patches of *Bouteloua curtipendula* Michx. (side-oats grama). Data from these two sites were used for qualitative comparisons and were not included in the statistical analyses.

### 2.4. Soil collection

Soils were collected from the landfill treatment plots on October 2003 and March, June, and September of 2004 and 2005. The two reference grasslands were sampled in September of 2004 and 2005. From each treatment plot, 10 soil samples (0–10 cm) were collected randomly, bulked into a single sample, mixed thoroughly, and placed in a cooler for transport. Gravimetric water content was determined on an aliquot of each soil sample to express nematode densities by soil dry weight (per kg of soil). Nematodes were extracted within 24 h from a 50 g aliquot of each soil sample using a modified Baermann funnel technique. The Baermann funnel procedure was modified to ensure collection of nematodes along the funnel sides (J. Starr, personal communication). Rather than removing a portion of the water from the funnel, this modification replaces all water within the funnel every 24 h. At each replacement, nematodes were concentrated using a 25 μm sieve and then held in a beaker. After 72 h, extracted nematodes were preserved in 5% formalin. All nematodes within a sample were identified to family and enumerated using an inverted microscope at 40× magnification. Feeding habits were assigned to nematode families according to Yeates et al. (1993), with the exception of root-tip feeders, which were placed in the fungal feeders group as recommended by Forge et al. (2003).

### 2.5. Nematode community indexes

Nematode communities were characterized using several different indexes that describe their structure and function. Nematode diversity was evaluated using family richness, the Simpson Index of Dominance ($D = 1/\Sigma p_i^2$) and Shannon–Weaver Index of Diversity ($H' = \Sigma p_i \ln p_i$) (Shannon and Weaver, 1949; Simpson, 1949).

The Plant Parasite Index (PPI) and the Maturity Index (MI) were used to characterize the successional stage of the plant consuming and detritus channel portions of the soil nematode communities (Bongers, 1990; Yeates, 1994). These indexes assign nematode families within each group a ‘cp value’ based on its reproductive capacity and response to disturbance: low values are assigned to rapid colonizers and values up to a maximum of 5, representing increasing sensitivity to disturbance. For each sample, these indexes are calculated for the appropriate nematode group using the formula $\Sigma v_i f_i$, where $v_i$ is the cp value of the $i$th taxa, and the $f_i$ is the frequency of the $i$th taxa in the sample (Bongers, 1990). Lower values of PPI and MI indicate the relative dominance of colonizing nematode families.

Ferris et al. (2001) extended the trophic group concept and the Maturity Index into a single tool to evaluate the soil community: Weighted Faunal Index. This qualitative evaluation technique characterizes the nematode community using three indexes: Channel, Enrichment and Structure (Ferris et al., 2001). The Channel Index (CI) evaluates the relative importance of more conservative, predominantly fungal feeding nematodes to the opportunistic bacteria- and fungi-feeding nematodes (Kardol et al., 2005) and is more reliable than the ratio of fungivores to bacterivorous nematodes (Ruess, 2003). CI is calculated as: $\mathrm{CI} = 100(k_e Fu_2)/((k_e Ba_1) + (k_e Fu_2))$, where $Ba_1$ and $Fu_2$ are the percentages of opportunistic bacterivorous and fungivore grazers, respectively, and $k_e$ represents the enrichment rankings (Ferris et al., 2001) of each of these guilds. High values of CI indicate that fungivore nematodes predominate.

Within the Weighted Faunal Profiles the Enrichment Index (EI) considers nematode groups that respond to increased resource availability (Ferris et al., 2001). This index is calculated as: $\mathrm{EI} = 100(e/(e+b))$, where $b = \Sigma k_b n_b$ and $e = \Sigma k_e n_e$, $k$ is the weight given to each guild and $n$ is the density of nematodes within that guild. Nematode communities with high EI values are responding to increased resource availability.

The Structure Index (SI) assesses the degree of maturation of the soil food web by emphasizing nematode guilds that require environmental stability for increased population growth. Over time, this index characterizes succession within the soil fauna (Ferris et al., 2001). The Structure Index is calculated as: $\mathrm{SI} = 100(s/(s+b))$, where $b = \Sigma k_b n_b$ and $s = \Sigma k_s n_s$, $k$ is the weight given to each guild and $n$ is the density of nematodes within that guild. Nematode communities that are recovering from stress or disturbance have greater SI values (Ferris et al., 2001).

### 2.6. *Plant density*

Plant density was determined for the landfill site in August 2003, and in May and September of 2004 and 2005. All plants were identified and enumerated within 10 randomly placed 0.25-m$^2$ quadrats within each treatment plot ($n = 300$). Spring samples included winter annuals, cool-season grasses (predominantly $C_3$), legumes, and spring blooming perennials. Fall samples included summer blooming perennials and warm-season grasses (predominantly $C_4$). The contribution of the removed individuals of *A. trifida* and *H. annuus* was determined from enumerating individuals with in 0.25-m$^2$ quadrats prior to removal. These data were added to the fall 2003 density data. The densities of plants in each functional group (grasses, forbs, and legumes) were averaged to the plot level prior to statistical analysis.

### 2.7. *Statistical analyses*

Initial statistical analysis showed no significant block effects due to slope position and, therefore, this was removed from subsequent statistical analyses. Nematode community and plant density data were analyzed with a repeated-measures analysis within the linear mixed models procedure (Piepho et al., 2003). Nematode density data were log-transformed ($\ln + 1$) to meet assumptions of normality and equality of variance; back-transformed data are presented. Index values were not transformed. Akaike's Information Criterion (AIC) was used to determine the optimal covariance structure, which was AR1 (Uzoh and Oliver, 2006). The model included three fixed terms, amount, location and time, as well as their interactions (Piepho et al., 2003). Least Squares Difference post-hoc tests were used to determine differences within response variables. Significance was declared at the 0.05 level. Data were analyzed using SPSS 13.0.1 (SPSS Inc. Chicago, Illinois, USA).

## 3. Results

### 3.1. *Nematode diversity and density*

A total of 20 nematode families were observed in the landfill restoration experiment. Bacterivorous families observed included Alaimidae, Cephalobidae, Monhysteridae, Plectidae, and Rhabditidae. Fungivorous and root-tip feeding taxa included Aphelenchidae, Aphelenchoididae, Anguinidae, Leptonchidae, Psilenchidae, and Tylenchidae. Omnivorous families included Dorylaimidae. Plant parasitic families included Belondiridae, Heteroderidae, Hoplolaimidae, Longidoridae, Neotylenchidae, Paratylenchidae, and Pratylenchidae. Mononchidae was the only predatory taxa observed in this experiment. Family richness per sample ranged from 7 to 18.

Neither the amount nor location of organic amendments influenced nematode family diversity, dominance or richness, although these indexes varied significantly over time. Family richness increased throughout the experiment and was the highest in June 2005 (Table 2). Both the Simpson and Shannon–Weaver Indexes varied over time, but were lowest in June 2004, when the samples were dominated (45%) by a single family of plant parasitic nematodes (Hoplolaimidae) (Table 2).

Total density of nematodes kg$^{-1}$ soil was not affected by the amendment treatments, but differed significantly over time; total nematode density was similar in March and September 2005, but otherwise each sampling period was significantly different than the others (Tables 2 and 3). With the exception of the June sample period, there was an overall trend towards greater total nematode density over time.

Densities of nematodes within the different feeding groups changed significantly over time (Tables 2 and 3) and some of these trophic groups were also affected by the amendment location treatments. Bacterivorous nematode density was significantly greater in the surface plots (1740 ± 129 nematodes kg$^{-1}$ soil) than in the incorporated plots (1367 ± 103 nematodes kg$^{-1}$ soil) when averaged over the duration of the experiment. Similarly, omnivorous and predatory nematode density was greater in the surface

**Table 2**
Summary of nematode data from the experiment at the Castle Drive Landfill, Garland, Texas (mean ± SE, $n = 30$)

| | Oct. 2003 | Mar. 2004 | June 2004 | Sept. 2004 | Mar 2005 | June 2005 | Sept. 2005 |
|---|---|---|---|---|---|---|---|
| Nematode diversity indexes | | | | | | | |
| Family richness | 12.3 ± 0.3 | 11.7 ± 0.3 | 12.9 ± 0.3 | 13.8 ± 0.3 | 14.8 ± 0.2 | 15.6 ± 0.2 | 14.8 ± 0.2 |
| Simpson's index of evenness | 6.9 ± 0.3 | 6.0 ± 0.3 | 1.7 ± 0.3 | 5.0 ± 0.3 | 3.9 ± 0.3 | 4.2 ± 0.3 | 4.1 ± 0.3 |
| Shannon–Weaver index | 2.2 ± 0.1 | 2.0 ± 0.1 | 0.7 ± 0.1 | 2.0 ± 0.1 | 1.8 ± 0.1 | 1.9 ± 0.1 | 1.9 ± 0.1 |
| Nematode density kg$^{-1}$ soil | | | | | | | |
| Total nematodes | 2215 ± 223 | 2910 ± 292 | 48,068 ± 5014 | 5830 ± 578 | 12,553 ± 1238 | 17,449 ± 1754 | 11,507 ± 1135 |
| Bacterivorous nematodes | 445 ± 78 | 886 ± 155 | 2028 ± 260 | 1473 ± 180 | 2625 ± 317 | 3525 ± 434 | 1884 ± 229 |
| Fungi/root-tip feeding nematodes | 599 ± 86 | 579 ± 83 | 1600 ± 170 | 1185 ± 120 | 1795 ± 179 | 3323 ± 332 | 2248 ± 222 |
| Plant parasitic nematodes | 852 ± 156 | 1156 ± 211 | 39,848 ± 4987 | 1800 ± 232 | 6803 ± 859 | 8764 ± 1131 | 5853 ± 740 |
| Omnivorous nematodes | 164 ± 32 | 133 ± 27 | 106 ± 22 | 784 ± 145 | 614 ± 114 | 986 ± 183 | 969 ± 184 |
| Predatory nematodes | 1.4 ± 0.9 | 2.1 ± 1.4 | 9.0 ± 3.8 | 0.7 ± 0.7 | 26.5 ± 0.9 | 31.9 ± 8.2 | 7.1 ± 0.3 |
| Nematode community indexes | | | | | | | |
| Maturity index | 1.5 ± 0.1 | 1.3 ± 0.1 | 0.2 ± 0.06 | 1.5 ± 0.1 | 0.9 ± 0.06 | 1.1 ± 0.1 | 1.2 ± 0.1 |
| Plant parasite index | 1.3 ± 0.1 | 1.3 ± 0.1 | 2.7 ± 0.1 | 1.1 ± 0.1 | 1.8 ± 0.1 | 1.6 ± 0.1 | 1.6 ± 0.1 |

**Table 3**
Summary of linear mixed model analyses (F values) of the nematode data from the experiment at the Castle Drive Landfill, Garland, Texas

| | Loc | Rate | Time | Loc*rate | Loc*time | Rate*time | Loc*rate*time |
|---|---|---|---|---|---|---|---|
| Nematode diversity indexes | | | | | | | |
| Family richness | 3.3 | 2.3 | 29.6*** | 1.2 | 1.2 | 1.5 | 0.9 |
| Simpson's index of evenness | 1.2 | 0.5 | 33.0*** | 1.1 | 1.9 | 1.0 | 1.3 |
| Shannon–Weaver index | 2.9 | 0.8 | 79.5*** | 0.4 | 1.9 | 0.8 | 1.3 |
| Nematode density $kg^{-1}$ soil | | | | | | | |
| Total nematodes | 3.3 | 0.98 | 111*** | 0.29 | 0.87 | 1.1 | 0.9 |
| Bacterivorous nematodes | 5.7* | 0.98 | 31.2*** | 0.27 | 1.1 | 1.7 | 1.2 |
| Fungi/root-tip feeding nematodes | 3.5 | 2.1 | 44.1*** | 0.13 | 0.97 | 1.9 | 1 |
| Plant parasitic nematodes | 1.5 | 0.1 | 120*** | 1.0 | 2.2* | 0.8 | 0.9 |
| Omnivorous nematodes | 10.3** | 2.7 | 48.5*** | 0.1 | 0.5 | 0.3 | 0.7 |
| Predatory nematodes | 5.3* | 1.7 | 8.9*** | 0.3 | 0.8 | 1.1 | 1.4 |
| Nematode community indexes | | | | | | | |
| Maturity index | 0.29 | 0.42 | 102*** | 1.44 | 1.67 | 1.44 | 1.1 |
| Plant parasite index | 0.14 | 0.16 | 95.3*** | 1.3 | 1.76 | 1.67 | 1.0 |

Asterisks indicate degree of significance (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$).

plots (456 ± 41 omnivore and 6.0 ± 1.1 predator nematodes $kg^{-1}$ soil) compared to the incorporated plots (318 ± 30 omnivore and 2.9 ± 0.8 predator nematodes $kg^{-1}$ soil). The density of fungivorous and root-tip feeding nematodes were not affected by the amendment treatments. Plant parasitic nematodes were the dominant trophic group in each sampling period and comprised over 50% of the total nematode population in June 2004 and throughout 2005 (Table 2). The interaction of location and time was significant for this group because in March 2004 their density was greater in the surface treatments (1616 ± 294 nematodes $kg^{-1}$ soil) than in the incorporated treatments (699 ± 131 nematodes $kg^{-1}$ soil).

### 3.2. Nematode functional indexes

The interaction of amendment location and time was significant for CI, which was greater in the incorporated treatments. This treatment effect attenuated after June 2004, when the location treatments converge (Fig. 2a). The interaction between time and location was also significant for EI, which distinguished among amendment locations until September 2004, when this treatment effect was also no longer apparent (Fig. 2b). Amendment rate was also significant for EI with the control plots having significantly lower values (54.0 ± 1.3) than either the light (58.4 ± 1.3) or heavy (58.0 ± 1.3) amendment treatments when averaged over the 3 years of the experiment. Only time was significant for the Structure Index.

Weighted Faunal Profiles (Ferris et al., 2001) indicate that the quality of the nematode community in the landfill experiment changed over time (Fig. 3). In October 2003 the nematode community was in the undisturbed/stable quadrant. The community became less structured through June 2004. In September 2004, the nematode community had an increase in the EI, which subsequently fell throughout 2005. There was also an increase in the Structure Index from June 2004 to September 2004, but this also decreased during 2005.

Neither PPI nor MI was affected by the amendment treatments, but these indicators varied over time (Tables 2 and 3). The PPI was greatest during June 2004, where it was influenced by a high density of individuals in the Hoplolaimidae family (45% of total nematodes), and lowest in September 2004. PPI values from October 2003 and March 2004 were similar to each other, as were values from March through September 2005. MI values were more variable than the PPI over time and were lowest in June 2004.

### 3.3. Plant density

Total plant density was significantly affected by time and amendment location; the surface treatments had significantly greater plant density than the incorporated treatments, but this is only clearly evident in May 2004 (Fig. 4d). Time and amendment location significantly influenced grass density, with the surface treatments having significantly higher grass density than the incorporated plots (Fig. 4a). Time was the only significant factor for

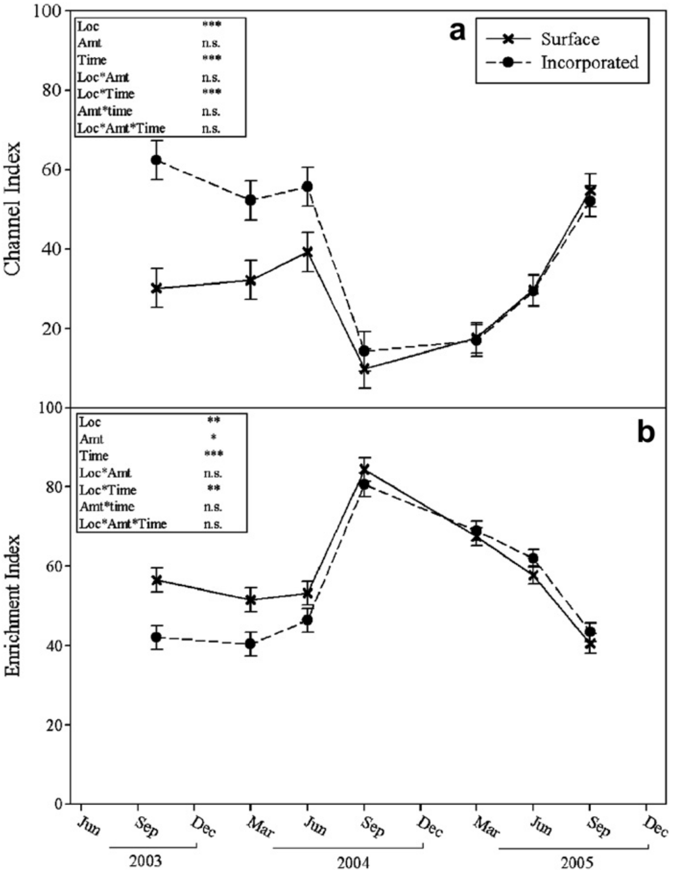

**Fig. 2.** Channel Index (CI) (a) and Enrichment Index (EI) (mean ± SE, $n = 15$) of the surface and incorporated treatments averaged for all the amendment rates over time. In the ANOVA table, loc = location of the organic amendment, and amt = amount of amendment applied.

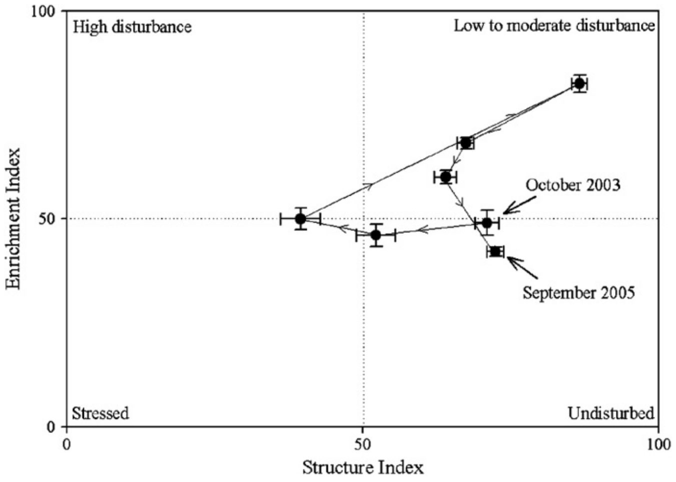

**Fig. 3.** Mean nematode Weighted Faunal Profiles (see Ferris et al., 2001) along axes of structure (SI) and enrichment (EI) over time (mean ± SE, $n = 30$) in the landfill experiment.

both legume density (Fig. 4b) and non-legume forb density (Fig. 4c), which contained many unplanted species.

### 3.4. Reference grasslands

Summary data from the native and restored reference grasslands at Rosehill Park are presented in Table 4. The EI values decreased in both the native and restored reference nematode communities between September 2004 and September 2005 (Fig. 5). CI values increased over this same interval. The low CI values at the restored reference in 2004 were influenced by high densities of individuals from the Monhysteridae family, which are ruderal bacterivorous nematodes.

Total nematode population size at the landfill experiment was lower than the native grassland reference, and was similar or slightly larger than total populations at the restored grassland reference at Rosehill Park (Tables 2 and 4). In contrast, the density of plant parasites was larger in the landfill experiment than the Rosehill reference grasslands. PPI values corresponded to these differences and were lower in the reference grasslands than in the landfill experiment in September 2005.

## 4. Discussion

Neither the amount nor location of organic amendment had an effect on nematode family richness, diversity or total nematode density during the 3 years of this study. Slow nematode migration rates and the homogeneous nature of the amendment material (Ilieva-Makulec et al., 2006) may have contributed to the lack of treatment-induced diversification in nematode community. This limited differentiation is congruent with other studies reporting slow synchronization of soil fauna diversity and resources after restoration or other management (Wardle et al., 1995; Li et al., 2007).

Despite the lack of diversity differences, both feeding group composition and the relative importance of the indicators EI and CI were affected by the amendment location treatment in this study. These treatment-induced differences, however, were contrary to our hypotheses. We expected that the spatial separation of the surface amendment and soil would favor conservative nematode groups, such as fungivores; while the treatments with imbedded amendments would favor groups that respond rapidly to resource enrichment, such as bacterivorous nematodes (Beare et al., 1992; Fu et al., 2000). Instead, we found that the surface treatments that had a greater density of bacterivorous nematodes and had community index values indicating relatively greater resource availability and decomposition dominated by bacteria and other opportunistic decomposers (Fig. 2). Similarly, the CI and EI in the incorporated treatments indicated relatively lower resource availability and decomposition dominated by fungi (Kardol et al., 2005) relative to the surface treatments.

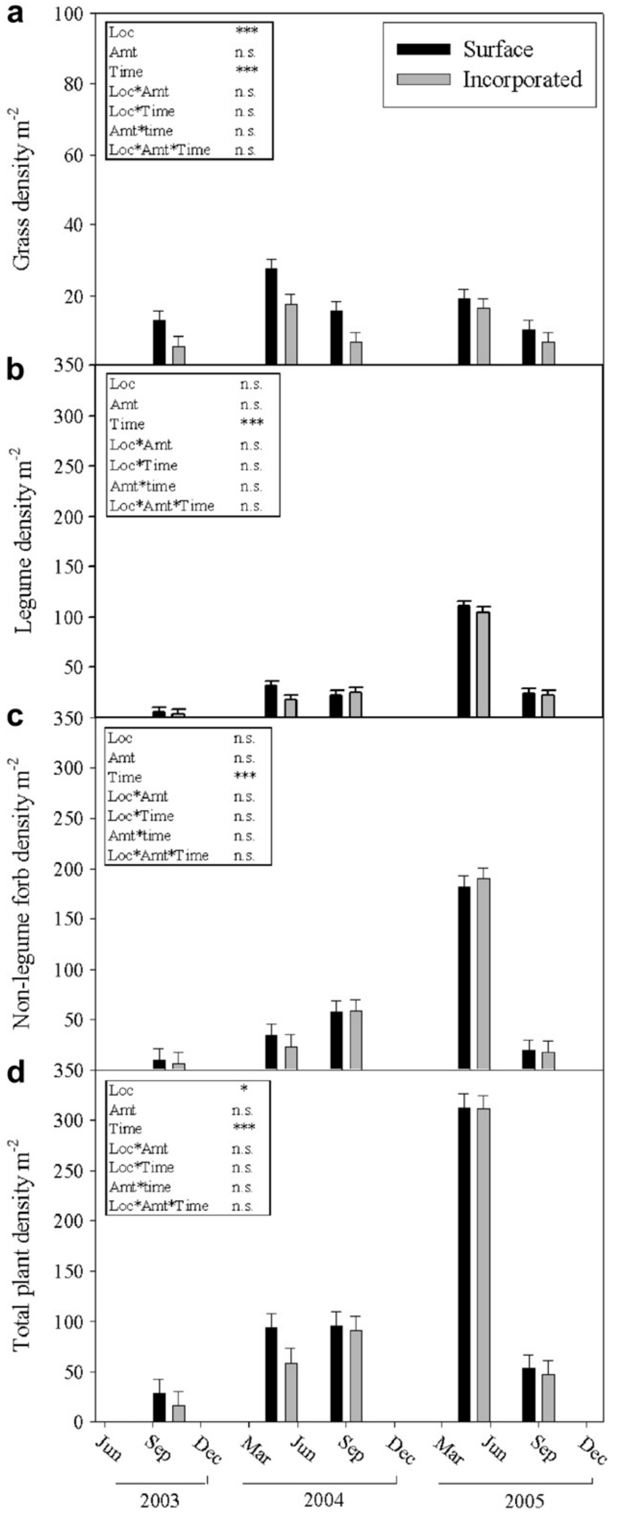

**Fig. 4.** Grass (a), legume (b), non-legume forb (c) and total plant density (d) of the surface and incorporated treatments for all amendment rates (mean ± SE, $n = 15$). Abbreviations in ANOVA tables are the same as in Fig. 2.

**Table 4**
Summary of nematode and soil nutrient data from the native and restored reference grasslands at Rosehill park, Garland, Texas (mean ± SE, $n = 2$) in September of 2004 and 2005

| | Native | | Restored | |
|---|---|---|---|---|
| | 2004 | 2005 | 2004 | 2005 |
| Soil nutrients | | | | |
| Soil organic carbon (g C kg$^{-1}$ soil) | ND | 4.1 ± 0.2 | ND | 1.7 ± 0.2 |
| Soil total nitrogen (g N kg$^{-1}$ soil) | ND | 0.34 ± 0.01 | ND | 0.13 ± 0.02 |
| Soil microbial biomass-carbon (g C kg$^{-1}$ soil) | ND | 2.8 ± 0.2 | ND | 1.5 ± 0.1 |
| Nematode community indexes | | | | |
| Family richness | 14.5 ± 0.5 | 18.5 ± 1.5 | 15.0 ± 1.5 | 14.5 ± 1.5 |
| Simpson's index of evenness | 5.4 ± 1.5 | 7.1 ± 0.7 | 8.9 ± 1.2 | 5.1 ± 1.3 |
| Shannon–Weaver index | 2.2 ± 0.3 | 2.3 ± 0.1 | 2.4 ± 0.3 | 1.9 ± 0.3 |
| Nematode density kg$^{-1}$ soil | | | | |
| Total nematodes | 10,349 ± 3045 | 13,201 ± 4752 | 4102 ± 2100 | 6451 ± 2123 |
| Bacterivorous nematodes | 3120 ± 2452 | 3117 ± 1808 | 1113 ± 501 | 458 ± 29 |
| Fungi/root-tip feeding nematodes | 4660 ± 3531 | 6705 ± 2335 | 1397 ± 560 | 2747 ± 310 |
| Plant parasitic nematodes | 1648 ± 1221 | 2313 ± 193 | 611 ± 502 | 1860 ± 1490 |
| Omnivorous nematodes | 861 ± 680 | 1059 ± 435 | 785 ± 382 | 1371 ± 279 |
| Predatory nematodes | 0 | 7.8 ± 7.8 | 0 | 13.5 ± 13.5 |
| Nematode community indexes | | | | |
| Maturity index | 1.7 ± 0.2 | 1.5 ± 0.1 | 1.9 ± 0.1 | 2.3 ± 0.04 |
| Plant parasite index | 0.80 ± 0.5 | 1.1 ± 0.1 | 0.83 ± 0.1 | 1.0 ± 0.2 |
| Channel index | 35.9 ± 1.1 | 85.1 ± 15.0 | 7.7 ± 15.1 | 42.7 ± 38.2 |

There are several possible reasons for the departure from our hypotheses. First, it is likely that the plant community's response to the amendments may have altered interactions among detritivores and complicated the treatment effects on the nematode community (Setala et al., 1998). Both total and grass plant density were greater in the surface amended plots (Fig. 4a and d), suggesting the potential for greater inputs of relatively labile carbon in the form of root exudates and/or root detritus, which may have favored bacteria. In fact, soil microbial biomass was greater in the surface treatments (0.96 ± 0.02 g C kg$^{-1}$ soil) compared to the incorporated treatments (0.88 ± 0.02 g C kg$^{-1}$ soil) when averaged over 3 years of monitoring (Biederman, unpublished observation). Other studies have found similar correlations between bacterivorous nematode density (or those indexes that correspond to their activity) and plant growth (Ferris et al., 1998; Viketoft et al., 2005). Direct measures of nematode potential food sources, such as characterization of soil microbial community composition by phospholipid fatty acid (PLFA) analysis, would further elucidate the soil ecosystem's response to both vegetation and the amendment treatments.

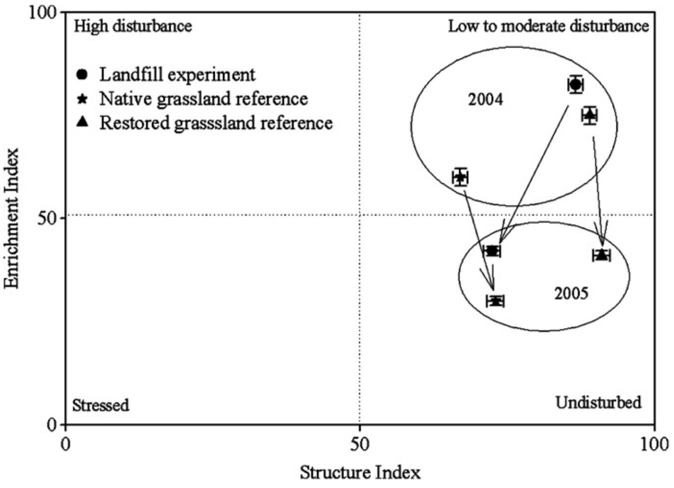

**Fig. 5.** Mean nematode Weighted Faunal Profiles along axes of structure (SI) and enrichment (EI) for September 2004 and September 2005 for the landfill experiment (mean ± SE, $n = 30$) and the native and restored reference grasslands at Rosehill Park (mean ± SE, $n = 2$).

Second, subtle differences in the microenvironment created by the addition of amendment may be overriding expectations based on the role of organic amendments as a carbon source for belowground biota. For example, surface amendments can reduce incident radiation to the soil surface, thus moderating soil temperature extremes and lessening soil moisture loss (Tian et al., 1993; Price et al., 1998). These microenvironmental conditions may be driving the increased nematode population size and facilitating the activities of soil organisms in the surface treatments.

Third, variation in the regional environment, such as climate or plant phenology, may be overwhelming the ability of the management treatments to influence the nematode community (Todd et al., 2006). Prairie ecosystems are disturbance-adapted (Todd, 1996; Rice et al., 1998) and the nematode fauna may be more reactive to regional patterns of precipitation or other environmental factors, rather than the localized effect of the restoration treatments (Neher et al., 2005). For example, it is unclear if the increase in CI in the landfill soils from September 2004 to September 2005 is the result of succession to more conservative groups or a response to drier climate conditions, which also favors fungi-feeding nematodes (Griffiths, 1995). Likewise, similar temporal shifts in the Weighted Faunal Profiles at the two reference grasslands at Rosehill Park compared to the landfill experiment from September 2004 to September 2005 (Fig. 5) suggest that the nematode communities present at all of these site are responding to some regional environmental factor such as climatic variation.

### 4.1. Importance of plant parasitic nematodes during restoration

Although there were broad similarities in the Weighted Faunal Profiles between the landfill experiment and the reference grasslands (Fig. 5), differences in the distribution of feeding groups suggest that the landfill experiment may not be at equilibrium. Specifically, plant parasitic nematodes comprised an unexpectedly large proportion of the nematode community at the landfill experiment (37% in 2004 and 52% in 2005) compared to either the native (16% in 2004 and 17% in 2005) or restored (15% in 2004 and 29% in 2005) grassland communities at Rosehill Park. Likewise, the PPI was greater at the landfill experiment than those of the reference grasslands in September 2005 (Tables 2 and 4). This was unexpected because large populations of plant parasitic nematodes are not well-documented in restoration projects concerned with primary succession. Instead, there is an expectation that the detrital-feeding organisms arrive earlier in succession because "their table is set early", and community development is supported by indigenous carbon sources rather than plant inputs (Bongers, 1990; Hodkinson et al., 2002). For example, Dmowska (2005) found low levels of plant parasitic nematodes under meadow vegetation upon reclaimed Polish ash dumps, and Stanton and Krementz (1982) found lower densities of plant parasitic nematodes on reclaimed mines with desert shrub vegetation than in nearby native sites. Pathogen loads, such as populations of plant parasitic nematodes, are generally thought to increase with time during succession (Van der Putten et al., 1993).

In contrast, other studies have found that plant/soil interactions, such as belowground herbivory, accelerated succession following land abandonment (Kardol et al., 2005). Korthals et al. (2001) found that plant parasites dominated early successional grasslands and decreased with time, possibly as a response to deeper and less palatable root systems. Populations of plant parasitic nematodes can also be promoted by a reduction of predatory nematodes (Sanchez-Moreno and Ferris, 2007), which tend to be sensitive to disturbance activities (Ferris et al., 2001). The timing of these plant/soil feedbacks may be important for controlling the rate of succession (Olff et al., 2000; Verschoor et al., 2002; De Deyn et al., 2003; Schadler et al., 2004) and their management in restoration may be required.

## 5. Conclusions

Although management of soil biological properties may increase the potential for success during ecological restoration, there are few restoration strategies that explicitly target their development. In this study, the amount and location organic amendment treatments had little influence on the nematode density or family diversity in the first 3 years of following management. Nematode community structure, however, was altered by the location of the amendments in a manner that was opposite of our expectations. The surface amendment treatments favored higher densities of bacterivorous, plant parasitic, omnivorous and predatory nematodes. Likewise, Channel Index and Enrichment Index values indicate that the nematode community of the surface treatments was dominated by opportunistic nematodes that respond rapidly to increased resource availability over the first 15 months of this study. The surface application of organic amendments also enabled the development of greater plant density. We suggest that this greater plant density favored opportunistic nematode groups, such as bacterivores, through increased inputs of high-quality organic matter (such as root exudates and/or detritus) to the soil. The very high densities of plant parasites at the landfill experiment in June 2004, as well as the larger proportion of this trophic group compared to nearby reference grasslands, further underscores the influence of plant resources in soil biota development during this study. Organic amendments can directly influence soil biota by altering potential food sources, or indirectly by altering the environment for plant community development and the availability of plant-derived resources to soil organisms; future studies need to determine relative importance of these two factors for ecosystem development in restoration.

## Acknowledgments

The authors acknowledge Grace Li and Diana Wall at Colorado State University for training in nematode identification; Andy Crane, Elizabeth Morgan and Jennifer Houseman for lab assistance; and James Starr, Forest Robinson, David Briske, Emily Hollister and the anonymous reviewers for greatly improving the manuscript. This research was supported by the City of Garland. The lead author was also supported by the Tom Slick Graduate Research Fellowship, the Francis and Evelyn Clark Soil Biology Scholarship from the Soil Science Society of America, the Franklin F. Wasko Graduate Research Fellowship, Springfield Research Funds and a Regents Graduate Fellowship. We acknowledge the City of Garland Parks Department for access to Rosehill Park.

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