

EFFECTS OF AGRICULTURAL PRACTICES IN THE RICE CROP SYSTEM ON NEMATODE COMMUNITIES IN URUGUAY

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Summary. An investigation was undertaken on the structure of the nematode community in the rice crop system by studying it under a rice crop, rotation prairie and improved natural prairie in Uruguay. Forty-nine genera of soil nematodes were identified. Bacterial-feeding nematodes were the most abundant in rice crops and in rotation prairie. Fungal-feeding, plant parasitic and predator nematodes occurred in large populations in improved natural prairie. Predator nematodes were not found in rice crops. Indices of richness and diversity were significantly different between prairies and rice crops. Analysis of correspondences showed that bacterial-feeding nematodes characterized the rice crop and that plant parasitic and predator nematodes characterized the improved natural prairie.

Key words: Trophic groups, bio-indicators, management practices, *Oryza sativa*.

Nematodes are widely distributed in the soil and their communities are large and rich in species. They play important roles in soil ecosystem processes; in particular, bacterial and fungal feeding nematodes regulate decomposition and nutrient cycling by releasing nutrients in forms available to plants (Ingham *et al.*, 1985; Neher, 2001). Thus, any disturbance that influences food resources or the environment is expected to modify the abundance and composition of nematode communities (Neher, 2001). Agricultural practices, and human intervention in general, are disturbances that affect the soil itself and the soil biota community (Yeates *et al.*, 1999; Neher, 1999, 2001). Soil nematodes have peculiarities that make them suitable as bio-indicator organisms to reflect soil health (Freckman, 1988; Bongers, 1990). Soil health is defined as “the capacity of a soil to function within an ecosystem, to sustain biological productivity, maintain environmental quality and promote plant and animal health” (Doran and Parkin, 1996).

Trophic categories and functional guilds have been used to develop a number of indices for assessing nematode diversity. Abundance of nematodes, trophic classification, Shannon-Weaver diversity, maturity index and others have all been used to varying degrees to assess soil management (Bongers, 1990; Ferris *et al.*, 2001; Yeates, 1999). It is recognized that nematodes of certain functional guilds are present in disturbed or stressed systems and that these basic community types can be compared with other nematode communities (Ferris *et al.*, 2001). Nutrient enriched soils show a reduced diversity; under

such conditions the populations of *r* strategists increase relative to other nematode groups (Freckman, 1988). Larger nematodes, often omnivores or predatory nematodes that are slower to reproduce and have longer life cycle (*K*-strategists), are dominant in more stable systems (Bongers and Bongers, 1998; Bongers and Ferris, 1999).

Crop-pasture rotations (CPR) have been the predominant cropping system in Uruguay since the 1960s. Under this management system, soil organic matter content is maintained or increased in relation to the initial level. Fertility, physical and chemical properties are improved quickly with inclusion of pasture in a crop rotation (García-Préchac *et al.*, 2004). In Uruguay there are no published studies on the effects of management practices on soil nematodes. The main hypothesis of the present study was that the structure of nematode communities would change following different agricultural practices of a rice crop-pasture rotation. To assess the effects of rice crop management, the nematode community was compared with those of rotation and improved natural prairies.

MATERIALS AND METHODS

Site and sampling. The study area is located in the Experimental Station Paso de la Laguna (33° 14' S, 54° 15' W), which belongs to INIA (National Institute of Farming Investigations) in Uruguay. The climate type according to Koeppen-Geiger classification is Cfa (Strahler and Strahler, 1992), i.e. temperate with precipitation throughout the year. Molisol is the predominant soil type in the experimental area. The median annual precipitation is 1292 mm and the median annual temperature is 17 °C.

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The experimental station has 80 ha of land, which is used for rice (*Oriza sativa* L.) crop-pasture rotation with no-till and improved natural prairies.

Three sites were selected on the basis of the level of disturbance: a rice crop (RC) with major disturbance, a rotation prairie (RP) with an intermediate level of disturbance, and an improved natural prairie (NP) with a minor level of disturbance.

The RC site was sown no-till in October 2000. During the growing cycle, the crop was fertilized three times with nitrogen (20, 23 and 23 kg NH₄NO₃ ha⁻¹) and once with phosphorus (50 kg P₂O₅ ha⁻¹) and received two applications of herbicide (byspiribac-sodium) and one of fungicide (azoxistrobin). The crop was waterlogged from December 2000 to March 2001 and harvested from March to April.

The RP site entered the pasture stage in March 2000, when it was sown no-till with *Lolium multiflorum* Lam., *Lotus corniculatus* L. and *Trifolium repens* L. Other plant species in this site are *Trifolium pratense* L., *Paspalum* sp. and *Setaria geniculata* P. Beauv. Both RC and RP were included in a rotational system consisting of two years of rice crops followed by four years of pastures (grasses and legumes) used for livestock (sheep and cattle) grazing in winter months.

The NP had never been utilized for rice cropping. It was sown with *Lotus subbiflorus* Lag. in May of 2000 and not fertilized or tilled. The principal plant species in this site were *Paspalum dilatatum* Poir., *P. notatum* Flügge, *Sporobolus indicus* (L.) R. Br., *Cynodon dactylon* (L.) Pers., *Vulpia australis* (Ness ex Steud.) C.H. Blom, *L. multiflorum*, *Adesmia bicolor* (Poir.) DC., *Eryngium horridum* Malme and *E. paniculatum* Cav. et Dombey ex F. Delaroche.

Sampling was carried out at the end of the rice growing season (from 3 to 5 April 2001). In each site, four plots of 100 m² were positioned randomly along a longitudinal transect. A total of ten soil cores (3 cm diameter and 15 cm depth) per plot were taken to compose a bulk sample. Soil nematodes were extracted from 100 g wet soil sub-samples, within a week of sampling, by the Whitehead and Hemming technique (Taylor, 1971), identified to genus and assigned to corresponding trophic groups (functional groups) according to Yeates *et al.* (1993). Soil moisture was determined after drying at 100 °C for 48 h.

Data analysis. Several indices were calculated to analyze the abundance and diversity of the nematode com-

munities in the three sites: genera density (Σ = number of genera per 100 g soil); abundance (N = total number of nematodes per 100 g soil); trophic diversity ($T = 1/\Sigma p_i^2$) where p_i is the proportion of trophic group i in the total population (Heip *et al.*, 1988); Shannon diversity index ($H' = -\Sigma p_i \ln p_i$) where p_i is the proportion of genera i in the total population; generic evenness ($J' = H'/H'_{\max}$) where H'_{\max} is $\ln \Sigma$; and the maturity index (ΣMI) proposed by Yeates (1994) for soil nematodes as a way to integrate their abundance and diversity based on the ecological characteristics of the taxa (colonizers versus persisters). ΣMI is calculated by the formula ($\Sigma MI = \Sigma n_i \times p_i$) where n_i is the c-p value of taxon i , and cp values 1-5 correspond to the position of the taxa on the perceived r - K strategy gradient as described by Bongers (1990), and where p_i is the proportion of individuals of genera i in the total population. The plant parasite index (PPI) was also calculated. This is an ecosystem parameter based on life history characteristics of plant parasitic nematodes coded as c-p values (Bongers, 1990).

The index values of the three sites were compared by one-way analysis of variance (ANOVA). When $P < 0.05$, differences were considered significant and values from the three sites were compared by Scheffe post-hoc test.

The relation of bacterial-feeding (B) to fungal-feeding (F) nematodes provides information on dominant organic matter decomposition pathway (Wasilewska, 1997a) (i.e. with participation of bacteria or fungi), consequently the nematode channel index $B/(B+F)$ was calculated. A high value of nematode channel index suggests a bacterial decomposer community and a low value suggests a fungal decomposer dominated nematode community.

A Correspondences analysis was used in order to relate the variables analyzed (nematode functional groups and sites) and to generate a hypothesis. We considered cosine² and relative inertia of variables for each axis. This analysis was applied on relative abundance higher or equal to 1% of each genus per site.

All statistical analyses were carried out with StatSoft Inc. (1999).

RESULTS

Soil moisture content was similar in the three sites: 34, 30 and 31% dry weight in RC, RP and NP, respectively.

Table I. Total abundance (specimens/100 g of soil per plot), mean and standard deviation per site.

| Site | Rice crops | | | | | Rotation prairie | | | | | Improved natural prairie | | | | |
|-----------------------------|--------------|-----|----|-----|-------|------------------|-----|-----|-----|-------|--------------------------|-----|-----|-----|-------|
| | 1 | 2 | 3 | 4 | Total | 1 | 2 | 3 | 4 | Total | 1 | 2 | 3 | 4 | Total |
| Plots | 1 | 2 | 3 | 4 | Total | 1 | 2 | 3 | 4 | Total | 1 | 2 | 3 | 4 | Total |
| Total abundance | 164 | 162 | 95 | 117 | 538 | 162 | 205 | 245 | 216 | 828 | 190 | 175 | 350 | 119 | 834 |
| Mean and standard deviation | 134.5 ± 34.1 | | | | | 207.0 ± 34.4 | | | | | 208.5 ± 99.2 | | | | |

Table II. Density (specimens/100 g of soil) of nematode taxa in the studied sites.

| Genus | RC1 | RC2 | RC3 | RC4 | RC total | RP1 | RP2 | RP3 | RP4 | RP total | NP1 | NP2 | NP3 | NP4 | NP total |
|--------------------------|-----|-----|-----|-----|----------|-----|-----|-----|-----|----------|-----|-----|-----|-----|----------|
| <i>Acrobeles</i> | 6 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 |
| <i>Acrobelloides</i> | 6 | 0 | 0 | 0 | 6 | 5 | 7 | 4 | 0 | 16 | 0 | 2 | 0 | 0 | 2 |
| <i>Anaplectus</i> | 3 | 0 | 0 | 0 | 3 | 0 | 7 | 3 | 0 | 10 | 0 | 0 | 6 | 0 | 6 |
| <i>Aphelenchoides</i> | 4 | 4 | 0 | 4 | 12 | 0 | 6 | 3 | 7 | 16 | 0 | 4 | 7 | 0 | 11 |
| <i>Aphelenchus</i> | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 |
| <i>Belonolaimus</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| <i>Boleodorus</i> | 0 | 2 | 0 | 0 | 2 | 0 | 0 | 5 | 3 | 8 | 0 | 0 | 0 | 0 | 0 |
| <i>Butlerius</i> | 9 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Cephalobus</i> * | 3 | 5 | 12 | 17 | 37 | 13 | 24 | 24 | 15 | 76 | 22 | 20 | 17 | 6 | 65 |
| <i>Chiloplacus</i> * | 0 | 0 | 0 | 0 | 0 | 10 | 4 | 8 | 0 | 22 | 0 | 0 | 0 | 0 | 0 |
| <i>Coomansus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 2 | 0 | 6 |
| <i>Criconemella</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 |
| <i>Cruzinema</i> | 6 | 0 | 0 | 0 | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Diphtherophora</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| <i>Diploscapter</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 |
| <i>Discolaimoides</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 4 | 0 | 0 | 2 | 0 | 2 |
| <i>Discolaimium</i> * | 0 | 0 | 0 | 0 | 0 | 1 | 6 | 13 | 7 | 27 | 12 | 7 | 8 | 6 | 33 |
| <i>Ditylenchus</i> * | 0 | 0 | 0 | 4 | 4 | 0 | 0 | 12 | 0 | 12 | 0 | 0 | 29 | 0 | 29 |
| <i>Dorylaimus</i> * | 3 | 15 | 7 | 13 | 38 | 2 | 24 | 14 | 21 | 61 | 8 | 14 | 18 | 5 | 45 |
| <i>Eucephalobus</i> * | 0 | 12 | 9 | 6 | 27 | 9 | 12 | 5 | 8 | 34 | 10 | 12 | 19 | 7 | 48 |
| <i>Eudorylaimus</i> * | 12 | 0 | 11 | 0 | 23 | 13 | 7 | 5 | 17 | 42 | 11 | 4 | 10 | 5 | 30 |
| <i>Filenchus</i> | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Helicotylenchus</i> * | 8 | 0 | 3 | 7 | 18 | 0 | 12 | 0 | 0 | 12 | 19 | 19 | 29 | 8 | 75 |
| <i>Hemicycliophora</i> | 9 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 2 |
| <i>Isolaimium</i> | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Heterodera</i> * | 0 | 0 | 0 | 0 | 0 | 19 | 12 | 32 | 18 | 81 | 18 | 12 | 58 | 21 | 109 |
| <i>Leptonchus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 |
| <i>Meloidogyne</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 4 |
| <i>Mesodorylaimus</i> * | 6 | 19 | 15 | 8 | 48 | 13 | 11 | 35 | 19 | 78 | 18 | 11 | 44 | 12 | 85 |
| <i>Mesorhabditis</i> * | 17 | 0 | 2 | 0 | 19 | 7 | 21 | 25 | 13 | 66 | 6 | 4 | 21 | 6 | 37 |
| <i>Mononchus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 |
| <i>Monbysteria</i> * | 0 | 25 | 0 | 2 | 27 | 0 | 3 | 0 | 0 | 3 | 5 | 10 | 4 | 0 | 19 |
| <i>Nygolaimellus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| <i>Nygolaimus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| <i>Nothotylenchus</i> | 2 | 6 | 0 | 2 | 10 | 0 | 0 | 0 | 1 | 1 | 3 | 5 | 0 | 5 | 13 |
| <i>Panagrolaimus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 12 | 12 | 0 | 0 | 2 | 1 | 3 |
| <i>Paraphelenchus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 0 |
| <i>Paratylenchus</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 2 |
| <i>Plectus</i> * | 3 | 10 | 3 | 9 | 25 | 9 | 6 | 7 | 0 | 22 | 0 | 0 | 0 | 0 | 0 |

Continued

Table II. Continuation.

| Genus | RC1 | RC2 | RC3 | RC4 | RC total | RP1 | RP2 | RP3 | RP4 | RP total | NP1 | NP2 | NP3 | NP4 | NP total |
|----------------------------|-----|-----|-----|-----|----------|-----|-----|-----|-----|----------|-----|-----|-----|-----|----------|
| <i>Pratylenchus</i> * | 9 | 13 | 9 | 7 | 38 | 6 | 0 | 0 | 0 | 6 | 4 | 10 | 0 | 0 | 14 |
| <i>Prismatolaimus</i> | 0 | 5 | 0 | 0 | 5 | 0 | 6 | 6 | 0 | 12 | 4 | 3 | 0 | 2 | 9 |
| <i>Psilenchus</i> | 0 | 2 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 |
| <i>Radopholus</i> | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 |
| <i>Rhabditis</i> * | 35 | 16 | 8 | 8 | 67 | 9 | 12 | 10 | 40 | 71 | 9 | 12 | 12 | 12 | 45 |
| <i>Teratocephalus</i> | 3 | 0 | 0 | 0 | 3 | 4 | 0 | 4 | 0 | 8 | 0 | 0 | 0 | 0 | 0 |
| <i>Tobrilus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 |
| <i>Tylencholaimellus</i> * | 0 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 9 | 5 | 3 | 16 | 4 | 28 |
| <i>Tylenchorhynchus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 4 |
| <i>Tylenchus</i> * | 17 | 27 | 16 | 30 | 90 | 24 | 25 | 30 | 23 | 102 | 30 | 10 | 42 | 15 | 97 |
| Total nematodes | 164 | 162 | 95 | 117 | 538 | 162 | 205 | 245 | 216 | 828 | 190 | 175 | 350 | 119 | 834 |

RC = Rice crops, RP = Rotation prairie, NP = Improved natural prairie, and 1, 2, 3 and 4 = number of plots.

* = Genera with relative abundance > 1% (considering all four plots).

Composition and structure of community. Total abundance was 2200 individuals in the study area. Even though the prairies were the most abundant systems (Table I), there were no significant differences in abundance between the three sites ($F_{(2,9)} = 1.79$; > 0.05).

A total of 49 genera were identified in the study area and greater richness was recorded from the prairies than from the rice crop (Table II and III).

The calculated indices of the studied sites are summarized in Table III. Indices of genus richness and trophic diversity were significantly different between prairies and rice crops ($F_{(2,9)} = 4.40$ and $F_{(2,9)} = 25.00$; < 0.05). The diversity index H' also showed significant differences in nematode faunae between prairies and RC ($F_{(2,9)} = 10.03$; < 0.05). Table IV shows the dominant genera in each site. Plant-associated nematodes of the

genus *Tylenchus* were dominant in the RC and in the RP (17 and 12%, respectively) and plant-parasitic nematodes of the genus *Heterodera* in the NP (13%). The

Table III. Indices of the nematode fauna in the studied sites: rice crop (RC), rotation prairie (RP) and improved natural prairie (NP).

| Index | RC | RP | NP |
|-----------------------------------------|------|------|------|
| Shannon diversity index (H') | 2.42 | 2.77 | 2.69 |
| Genus richness | 27 | 34 | 34 |
| Genus evenness (J') | 0.85 | 0.84 | 0.81 |
| Trophic diversity (T) | 3.41 | 3.73 | 4.81 |
| Σ Maturity index (ΣMI) | 2.40 | 2.60 | 2.76 |
| Plant parasite index (PPI) | 2.73 | 2.87 | 2.65 |

Table IV. Relative number (%) of the dominant nematode taxa (abundance > 5%) and their corresponding functional groups in the studied sites: rice crop, rotation prairie and improved natural prairie.

| Rice crops | | | Rotation prairie | | | Improved natural prairie | | |
|-----------------------|----|-------------------|-----------------------|----|-------------------|--------------------------|----|-------------------|
| Genus | % | Functional groups | Genus | % | Functional groups | Genus | % | Functional groups |
| <i>Tylenchus</i> | 17 | PA | <i>Tylenchus</i> | 12 | PA | <i>Heterodera</i> | 13 | PP |
| <i>Rhabditis</i> | 12 | BF | <i>Heterodera</i> | 10 | PP | <i>Tylenchus</i> | 12 | PA |
| <i>Mesodorylaimus</i> | 9 | O | <i>Mesodorylaimus</i> | 9 | O | <i>Mesodorylaimus</i> | 10 | O |
| <i>Pratylenchus</i> | 7 | PP | <i>Cephalobus</i> | 9 | BF | <i>Helicotylenchus</i> | 9 | PP |
| <i>Dorylaimus</i> | 7 | O | <i>Rhabditis</i> | 9 | BF | <i>Cephalobus</i> | 8 | BF |
| <i>Cephalobus</i> | 7 | BF | <i>Mesorhabditis</i> | 8 | BF | <i>Eucephalobus</i> | 6 | BF |
| <i>Monhystera</i> | 5 | BF | <i>Dorylaimus</i> | 7 | O | <i>Rhabditis</i> | 5 | BF |
| <i>Eucephalobus</i> | 5 | BF | <i>Eudorylaimus</i> | 5 | O | <i>Dorylaimus</i> | 5 | O |
| Total | 69 | | | 69 | | | 67 | |

BF = Bacterial-feeding nematodes, O = Omnivores, P = Predators, PA = Plant associated nematodes, and PP = Plant parasitic nematodes.

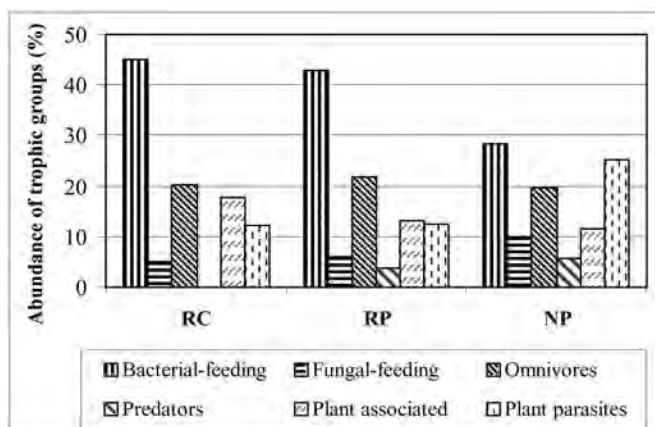
Table V. Density (N, individuals/100 g of soil) and relative abundance (%) of nematode trophic groups and Index B/(B+F) of three sites.

| Trophic groups | Rice crops (RC) | | Rotation Prairie (RP) | | Improved natural prairie (NP) | |
|-------------------|-----------------|----|-----------------------|----|-------------------------------|----|
| | N | % | N | % | N | % |
| Bacterial-feeding | 243 | 45 | 354 | 43 | 236 | 28 |
| Fungal-feeding | 26 | 5 | 50 | 6 | 83 | 10 |
| Omnivores | 109 | 20 | 181 | 22 | 162 | 19 |
| Predators | 0 | 0 | 31 | 4 | 46 | 6 |
| Plant-associated | 95 | 18 | 108 | 13 | 97 | 12 |
| Plant-parasites | 65 | 12 | 104 | 13 | 210 | 25 |
| Total | 538 | | 828 | | 834 | |
| B/(B+F) | 0.90 | | 0.88 | | 0.74 | |

Maturity indices (Σ MI) showed no significant differences in nematode fauna from the three sites ($F_{(2,9)} = 3.72$; > 0.05); however, these values were related to the degree of perturbation: the highest MI value was in NP, followed by RP and then RC. There were no significant differences in the plant parasite indices (PPI) ($F_{(2,9)} = 1.27$; > 0.05) (Table III).

Nematode functional groups. The six trophic groups described by Yeates *et al.* (1993) were represented in the prairies, there were no predator nematodes in the RC. The distribution of abundances of trophic groups differed significantly in the RC and the RP compared to the NP ($\chi^2 = 28.6$ and 16.6 ; $df = 5$; < 0.05 , respectively). The Trophic diversity index (T) was higher in the NP; analysis of variance showed significant differences in values of T between RC and NP ($F_{(2,9)} = 6.64$; < 0.05). The values of T showed the same tendency as Σ MI, inversely related to the degree of perturbation of sites (Table III).

Bacterial-feeding and predator nematodes were the most and the least abundant grouping, respectively, in the study area. The greatest abundances of bacterial-

**Fig. 1.** Distribution of abundance (individuals/100 g of soil, as percentages) of nematode trophic groups in the three sites: Rice crops (RC), Rotation prairie (RP) and Improved natural prairie (NP).**Table VI.** Results of Correspondence analysis. Eigenvalues, percentages of inertia explained and the contribution to the overall Chi-square. Total Chi-square = 222.24.

| Parameter | Axis 1 | Axis 2 |
|--------------------------------------|---------|--------|
| Eigenvalues | 0.058 | 0.023 |
| Percentages of inertia explained (%) | 55 | 22 |
| Chi squares | 122.217 | 48.034 |

feeding nematodes were in RC and RP, where they constituted about 40-45% of the total abundance. The greatest populations of fungal-feeding, plant parasitic and predator nematodes were in NP (Table V and Fig. 1). The B/B+F index increased from NP to RC, and bacterial-feeding nematodes were dominant in the disturbed site (Table V).

Figure 2 is a graphical representation of the Correspondence analysis. Two axes, which contributed 77% of the total variation and differentiated the sites, were extracted (Table VI). The first principal coordinate axis (55%) mainly separated plots of RC from plots of NP. Plots 2, 3 and 4 of RC (15, 7 and 6%, respectively), plot 2 of RP (12%), and plots 2, 3, and 4 of NP (9, 36 and 7%, respectively) were those that contributed most to the total inertia and were correlated with this axis (data not shown). The trophic groups that contributed most to the inertia in this axis were plant parasitic (41%), characterizing NP, and bacterial-feeding (23%), characterizing RC. The second axis contributed 22% to the total inertia. Predator (39%), plant associated (27%) and fungal-feeding (24%) nematodes were the trophic groups that contributed most to the inertia in this axis. However, only predator nematodes were correlated with axis 2 and they characterized plots of NP (Table VII).

DISCUSSION

The abundance of soil nematodes in the three sites was lower than values reported by Wasilewska (1979)

Table VII. Relative inertia, coordinates, cosine², and inertia of row variables (trophic groups).

| Trophic group | Relative inertia (%) | Coordinates | | Axis 1 | | Axis 2 | |
|-------------------|----------------------|-------------|--------|---------------------|---------|---------------------|---------|
| | | Axis 1 | Axis 2 | Cosine ² | Inertia | Cosine ² | Inertia |
| Bacterial-feeding | 17.20 | 0.189 | -0.075 | 0.718 | 0.225 | 0.114 | 0.091 |
| Fungal-feeding | 18.90 | -0.372 | 0.272 | 0.522 | 0.180 | 0.280 | 0.245 |
| Omnivores | 6.90 | 0.074 | -0.009 | 0.160 | 0.020 | 0.001 | 0.001 |
| Plant associated | 13.10 | 0.158 | 0.209 | 0.260 | 0.062 | 0.451 | 0.272 |
| Plant parasites | 17.70 | -0.370 | -0.017 | 0.871 | 0.414 | 0.002 | 0.002 |
| Predators | 26.10 | -0.398 | -0.492 | 0.310 | 0.099 | 0.674 | 0.388 |

and Yeates *et al.* (1997) in temperate agro-ecosystems of the northern hemisphere, where abundance can exceed 2000 specimens/100 g wet soil. These results cannot be compared to previous studies due to a lack of information on free-living nematodes in Uruguay. Total nematode abundance did not discriminate the different agricultural practices in this study, and the great variety of trophic functions and life strategies of soil nematodes may be responsible for these findings.

The number of genera we found was similar to the number recorded in pastures and in crops of the northern hemisphere (Wasilewska, 1979). The value was greater in prairies than in RC (34 and 27, respectively). The Shannon diversity index obtained here confirms the results given for managed grasslands dominated by *Lolium sp.* and *Trifolium repens* (Yeates, 1984) ($H' =$

2.0-2.7). Our results are similar to those obtained by Yeates (1984) and Yeates *et al.* (1991), who found that the diversity was able to distinguish different systems. They also confirmed that a greater diversity of nematode fauna exists in less disturbed soils (Norton, 1978).

Maturity indices have been widely used to investigate the effects of different kinds of disturbance on soil nematode fauna in natural prairies and agro-ecosystems (de Goede and Dekker, 1993; Freckman and Ettema, 1993; Pattison *et al.*, 2004). Low indices indicate large numbers of colonizers (short life cycle, high reproductive ratio, tolerance of perturbations), whereas high indices indicate a high degree of persistence in the population (long life cycle, low reproductive ratio, intolerance of perturbations). Agricultural practices, in general, result in disturbance of soil; however, the Maturity

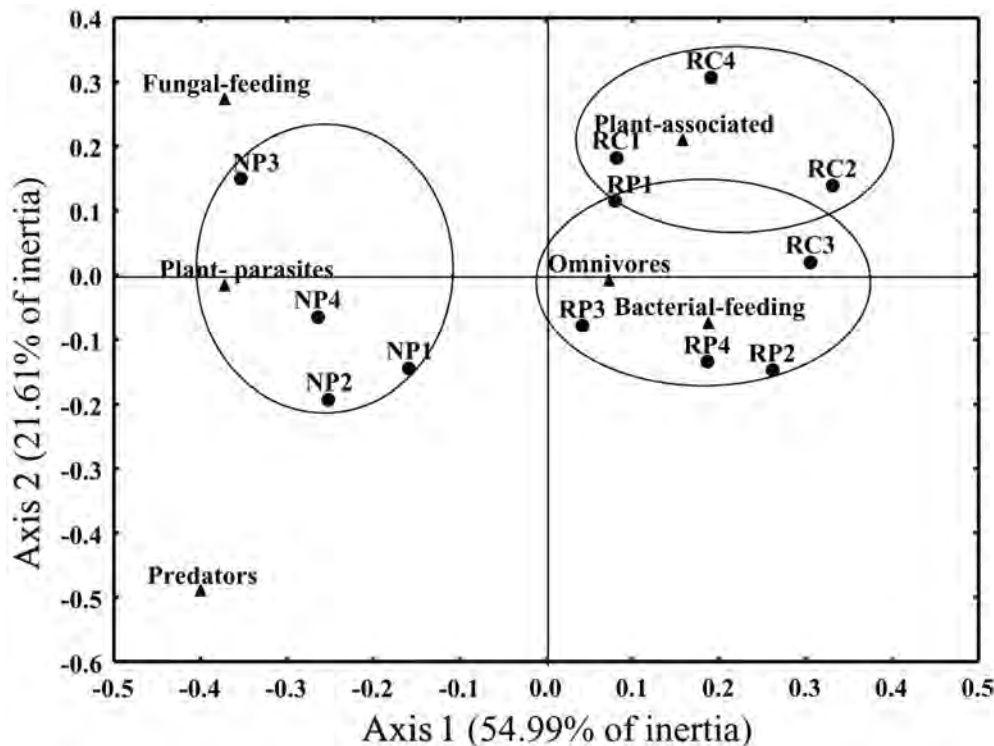


Fig. 2. Correspondence analysis. Ordination of trophic groups and plots of the studied sites on the two first axes. RC = Rice crops, RP = Rotation prairie, NP = Improved natural prairie and 1, 2, 3 and 4 = the numbers of the plots.

Index has not often been used as an ecological measure of such disturbance (Nombela *et al.*, 1998). In the present research it was possible to detect a gradient of perturbations from NP to RC. Thus, there was a progressive increase of site maturity as perturbation (water-logging, fertilization, effects of using machinery) was diminished. Nevertheless, the values of Σ MI of the three sites were lower than those found by Yeates and King (1997) in unmanaged prairies (Σ MI = 3.0-4.1) and by Wasilewska (1997b) and by Yeates *et al.* (1997) in agroecosystems (Σ MI = 2.2-2.5). Our data on plant parasite index (PPI) show values close to those published by Yeates and Bird (1994). There is no general agreement on the value of PPI as a measure of maturity of soils. Freckman and Ettema (1993) pointed out that PPI could potentially be more useful than MI to indicate system differences, but Bongers (1990) did not consider PPI as an index of disturbance. On the basis of our results, neither the Σ MI nor the PPI were useful for distinguishing differences between sites.

Soil structure of cultivated soils is very dynamic over time, so nematodes are exposed to a range of structural and chemical changes. In this research, bacterial-feeding nematodes comprised the majority of soil nematodes in the study area and in RC and RP, which are the most disturbed sites. Disturbance of soil usually results in an increase in microbial biomass. The increase of populations of bacteria due to tillage are well documented, and are due to organic residues, disruption of the physical structure of soil, and exposure of organic matter to microbial colonization (Feckman, 1988). In contrast, fungal-feeding nematodes were greatest in the NP. Didden *et al.* (1994) found increases in fungal-feeding nematodes with a change to "integrated" and less intensive management. This is because in the RC and RP fungal trophic resource was reduced by disturbance by machinery or by application of fungicides. In addition, poorly drained soils may be less favourable for fungal growth and grazing by fungivores compared to drained soils (Pattison *et al.*, 2004).

Plant feeding nematodes were more abundant in NP, probably because of the greater richness of plants (more habitats and resources) of this site. However, it is questionable how linked plant species diversity and soil nematode diversity are (Wasilewska, 1997a). Apparently, plant traits are more important than plant diversity in determining nematode abundance and activity in soil (Bardgett *et al.*, 1998). Another reason could be that the continuous presence of roots in the NP permitted an important increase in plant feeding nematodes. The persistence of root systems is more ephemeral due to use of machinery, which compacted the soil and removed roots in the other two systems. Sohlenius *et al.* (1987) and Neher (1999) argued that the absence of living roots during long periods of the year limited the growth of nematode populations, especially plant feeding nematodes. Also, according to Bongers (1990), Heteroderidae and *Helicotylenchus* indicate more stable habitats

and their relative abundances in NP were 13 and 9%, respectively (Table IV).

Omnivores and predators are relatively large nematodes and often are the most sensitive feeding groups with respect to tillage when annual cropping systems are compared with pastures (Wasilewska, 1979; Wardle *et al.*, 1995). The use of machinery causes compaction of soil, which results in loss of the pore space required for the movement of large nematodes. The compaction of soil has a negative effect on omnivores and predator nematodes (Ritz and Trudgill, 1999; Bouwman and Arts, 2000). Furthermore, flooding in RC promotes anaerobic conditions in the soil and results in the death of some nematode species. Saturated soil is unfavorable for most nematodes due to chemical properties of the soil solution as a result of microbiological activity (Simons, 1973). Jacq and Fortuner (1979) showed that some metabolites in soil of flooded rice fields in Senegal, under anaerobic conditions, reduced population levels of *Tylenchorhynchus martini* Fielding, *T. mashhoodi* Siddiqui *et* Basir, *Hirschmanniella oryzae* van Breda de Haan and *H. spinicaudata* Schuurmans Stekhoven. In our study, predators were the most affected functional group. The occurrence and abundance of different groups of nematodes have the potential to reflect soil physical conditions. Larger species of nematodes need interconnection of soil macropores for movement and trophic activities (Ritz and Trudgill, 1999). The absence of predators in RC may indicate greater alteration of the physical structure of the soil. The physical conditions of soil should be taken into account in future studies when trying to establish the effect of agriculture practices on nematofauna.

The relation of bacterial to fungal feeding nematodes is an indicator of the decomposition pathway (Sohlenius *et al.*, 1987; Yeates and Bongers, 1999). Our data suggest that in perturbed sites the bacterial decomposition pathway dominates, whereas the importance of fungal decomposition increases towards NP. These results are consistent with the domination of no-till systems by fungal decomposition (Hendrix *et al.*, 1986) and the domination of cropping and stressed systems by the bacterial pathway of decomposition (Pattison *et al.*, 2004).

Correspondence Analysis was useful to show changes due to the perturbation caused by agricultural practices and confirmed the above results, that predator and plant parasitic nematodes characterized NP whereas bacterial feeding nematodes characterized RC.

Although we considered only single examples of the three soil types, the results suggest that management practices of these soils can affect nematode functional groups. For future research, temporal factors must be taken into account when considering nematode diversity in agroecosystems.

Despite the limitations of our sampling operations, it is possible to infer that management practices of these soils affect nematodes functional groups. It is interesting to highlight that the different functional groups are

affected in different ways according to the level of disturbance. The results emphasize the importance of developing this kind of study in order to evaluate the bioindicator capacity of nematodes in different soils of Uruguay, and represent the first example of ecological research using soil nematodes in Uruguay.

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