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Applied Soil Ecology 4 (1996) 193–200

Applied Soil Ecology

Distribution of nematodes in vertisol aggregates under a permanent pasture in Martinique

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Accepted 13 May 1996

Abstract

This study reports on the distribution of nematodes in different soil habitats under a permanent pasture of digitgrass (*Digitaria decumbens* Stent. cv. 'Pangola') in Martinique. The objectives were (i) to evaluate a gentle fractionation method compatible with further soil nematode extraction and (ii) to assess the respective soil microhabitats of plant-feeding nematodes and free-living nematodes.

This study indicated that gentle soil fractionation can effectively separate soil habitats and allow the recovery of associated nematodes. Plant-feeding nematodes were equally distributed between inter-aggregate pores, habitats constituted of aggregated fine silt + clay particles and roots + rhizosphere. Most of free-living nematodes (53%) resided in inter-aggregate pores. Irrespective of the food resource, densities of nematodes (number per gram of habitat) were similar in habitats coarser than 1000 μm (A5000, A2000, and A1000). Habitats with the finest soil (A200) were not favourable sites because of the rarity of roots (for plant-feeding nematodes) and physical constraints.

Keywords: Nematode; Pasture; Soil aggregates; Soil fractionation; Soil habitats; Soil porosity; Vertisol

1. Introduction

Soils consist of an assemblage of solid particles and air-filled or water-filled pores of different sizes and shapes where microorganisms reside according to their feeding habits and physico-chemical constraints. Relations between soil environment and organisms have been widely reviewed (Smiles, 1988; Tisdall, 1991; Wolters, 1991; Lee and Foster, 1991; Juma, 1993; Oades, 1993). Gray and Williams (1971) indicated that carbon concentration controls the distribution of soil microorganisms. Griffin (1981) demonstrated the importance of water suction in microbial metabolism. Hassink et al. (1993) found a positive correlation between nematode biomass and the volume of pores 30–90 μm in diameter. Beare et al. (1995) developed a hierarchical model to describe the diversity of soil microhabitats in relation to biogeochemical cycling. One example of these relations can be illustrated by the results obtained by Hassink et al. (1993) where they found that grazing of bacteria by bacterivorous nematodes might explain differences in C/N ratios of soil organic matter in sandy soils and clay soils.

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PII S0929-1393(96)00118-7

Nematodes (free-living and plant parasitic) inhabit water-filled pore spaces. They occupy a specific niche in the food chain. Plant-parasitic nematodes affect plant productivity. Free-living nematodes interact with other microorganisms mainly through predation (Ingham et al., 1985). They are thought to be responsible for 30% of N mineralisation (Verhoef and Brussaard, 1990). Nematodes have been referred to as biological indicators (Freckman, 1988; Elliott, 1994). However, despite the extensive literature on soil nematodes and soil fertility, very little is known about the location of nematodes within soil aggregates.

To complement existing methods of evaluating relationships between soil structure and soil microorganisms (Jastrow and Miller, 1991; Darbyshire et al., 1993), this study investigated the performance of a gentle physical soil fractionation in nematode numeration in a vertisol with respect to soil aggregation. This highly aggregated soil also provided us with a good model to test the importance of the porosphere and the aggregatusphere (Beare et al., 1995) in nematode distribution.

2. Material and methods

2.1. Soil sampling

The study was conducted at Sainte-Anne, Martinique (Lesser Antilles: 14′3″N, 62′34″W). The soil was a vertisol (black earth) developed on volcanic ash, pH 4.8, organic carbon 5.4% and total nitrogen 0.42%. This tropical area is characterised by an annual rainfall of 1300 mm and a relative dry season of 4 months (March–June). The soil was under a 15-year-old pasture of digitgrass (*Digitaria decumbens* Stent, cv. 'Pangola'). Five adjacent plots (1 m^2) with similar soil features, depth (1 m) and slope (on the top) were wetted to pF 2 (60 g water g^{-1} soil) for 1 night prior to sampling, filling pores smaller than 30 μm in diameter (Haines, 1927).

The undisturbed soil top layer (3–8 cm) was sampled with a soil ring sampler (5 cm diameter, volume 98 cm^3, about 100 g of dry soil) in the root zone of the digitgrass. Two replicates were taken in the central area (625 cm^2) of each plot. One replicate was dedicated to the determination of weight of the habitats and the other to nematode enumeration.

2.2. Soil fractionation

Soil fractionation was carried out soon after soil sampling. Each undisturbed soil sample was submerged in distilled water (250 ml per 100 g dry soil), sufficient to fill pores larger than 30 μm in diameter. The samples were kept at 24°C for 36 h without agitation. Then, water in pores larger than 300 μm in diameter (macropore water) was emptied by suction (1 h at pF 1).

For each replicate, the weight (80°C oven-dried basis) of unfractionated soil was determined on a subsample prior to soil fractionation. The samples were gently fractionated by hand and by wet sieving and sedimentation (Chotte et al., 1994). Care was taken during soil fractionation to split the soil along natural planes of weakness and to remove small aggregates adhering to roots. The different fractions were: over 5000 μm diameter (A5000); 2000–5000 μm (A2000); 1000–2000 μm (A1000); 200–1000 μm (A200); 50–200 μm (A50); 0–50 μm (A0). The weight of each habitat was determined on an oven-dried (80°C) basis. The weights of each aggregate-class were summed and compared with the weight of unfractionated soil to test the efficiency of the fractionation. The fractionation schedule required 3 days for each set of five samples. Biological alterations, which would have occurred if soil samples had been stored pending fractionation, prevented us from taking more replicates.

The weight distribution of the habitats was compared with the weight (80°C oven-dried basis) of the simple mineral particles obtained by mechanical analysis after removal of organic cement by treatment with hydrogen peroxide (after Day, 1965). Particles larger than 50 μm were obtained by sieving, and particles less than 50 μm were analysed by a laser diffraction analyser (Malvern, Mastersizer/E).

2.3. Nematode extraction and identification

Nematodes were extracted from habitats larger than 50 μm (Fig. 1) by the elutriation–sieving technique (Seinhorst, 1962). Roots were rinsed with tap

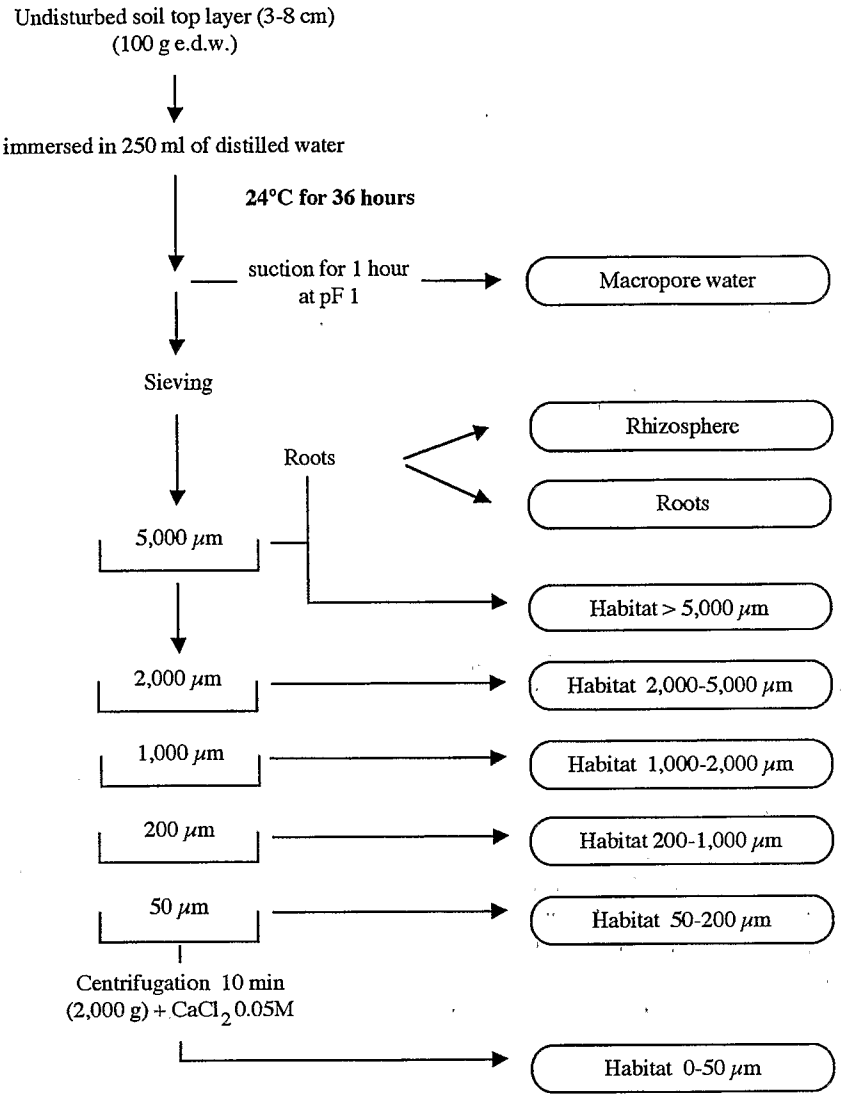


Fig. 1. Habitats analysed for nematodes.

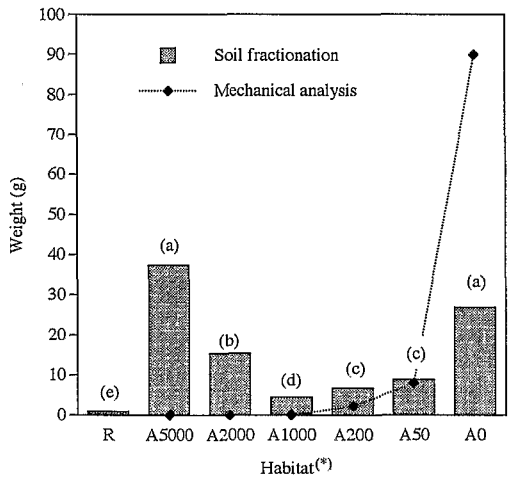
water (rhizosphere fraction) prior to nematode extraction in a mist-chamber for 2 weeks (Seinhorst, 1950). Nematodes were collected from liquid fractions, i.e. macropore water and rhizosphere fractions, on a bank of four 50-μm sieves, allowing total recovery of the nematodes present (Seinhorst, 1956). Similarly, soil sieving at 50 μm was repeated four times so that nematodes in habitats less than 50 μm (A0) were not assayed.

Nematode abundance was expressed as number per 100 g of unfractionated soil or per gram of habitat. Specific identifications were performed on fixed nematodes only for plant-feeding nematodes.

3. Results

3.1. Weight distribution of aggregates

No weight loss occurred on soil fractionation since weight recoveries after soil fractionation approximated 100% (e.g. 100.17%, 99.55%, 100.89%,



() two different letters indicated a significative difference (non parametric U Mann-Whitney test, $p < 0.05$)

* R: Roots.

A5000: Habitat > 5,000 μm
A2000: Habitat 2,000-5,000 μm
A1000: Habitat 1,000-2,000 μm
A200: Habitat 200-1,000 μm
A50: Habitat 50-200 μm
A0: Habitat < 50 μm

Fig. 2. Weight distribution of the fractions after soil fractionation and the simple mineral particles after mechanical analysis (results per 100 g of unfractionated soil).

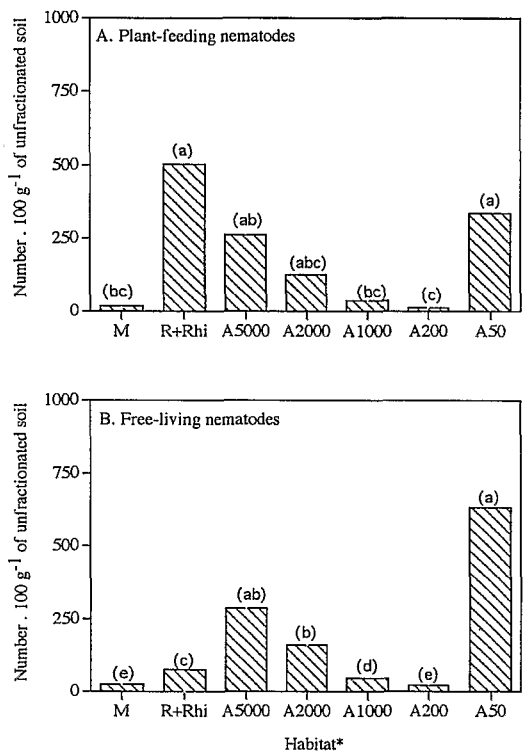
98.27%, and 101.09%). The Kruskal–Wallis test indicated that habitat weight differed significantly ($P < 0.001$). Comparison of mean weight among fractions (Mann–Whitney non-parametric U test) revealed that the weights of habitats A5000 and A0 were not significantly different at the $P < 0.05$ level (35 vs. 28 g per 100 g of unfractionated soil, respectively; Fig. 2). However, the weights of these habitats were significantly higher than those of the other fractions. Roots represented 0.9 g per 100 g of unfractionated soil. The A1000 habitat was the least abundant soil fraction, representing 5 g per 100 g of unfractionated soil, whereas habitats A200, A50 and A2000 amounted to 7 g, 9 g, and 15 g per 100 g of unfractionated soil, respectively.

In contrast to other habitats, the weight of habitat A0 was lower than that of the simple fine silt + clay particles obtained after the removal of organic matter and total dispersion of the soil, corresponding to only 30% of the weight of these particles. Thus, 70% of the fine silt + clay particles remained aggregated in coarser habitats.

3.2. Distribution of nematodes among habitats

Plant-feeding and free-living nematodes extracted from unfractionated soil were almost equally divided between plant-feeding (1300 individuals per 100 g of unfractionated soil) and free-living nematodes (1250 individuals per 100 g of unfractionated soil).

Plant-feeding nematodes comprised five different species. The two dominant species were the endoparasite *Pratylenchus zeae* and the ectoparasite *Tylenchus* sp., representing 73.1% and 26.7%, respectively, of the total plant-feeding nematodes. Three other species (less than 0.2%) were observed only



() two different letters indicated a significative difference (non parametric U Mann-Whitney test, $p < 0.05$)

* M: Macropore water
R+Rhi: Roots+Rhizospere

A5000: Habitat > 5,000 μm
A2000: Habitat 2,000-5,000 μm
A1000: Habitat 1,000-2,000 μm
A200: Habitat 200-1,000 μm
A50: Habitat 50-200 μm

Fig. 3. Distribution of plant-feeding nematodes (A) and free-living nematodes (B) in soil habitats.

rarely: *Meloidogyne incognita, Helicotylenchus retusus* and *Xiphinema setariae*. The numbers of plant-feeding nematodes in each habitat differed significantly (Kruskal–Wallis, $P < 0.05$). They were mostly recovered from the roots + rhizosphere fraction (503 individuals per 100 g of unfractionated soil; 39% of total), and habitat A50 (336 per 100 g of unfractionated soil; 26% of total) (Fig. 3). About 80% of the plant-feeding nematodes in the roots + rhizosphere fraction were represented by endoparasitic species (i.e. *Pratylenchus zeae)* inhabiting roots.

The numbers of plant-feeding nematodes in habitats A5000 and A2000 were not significantly different from those recovered from roots + rhizosphere and A50 (Mann–Whitney *U*-test, $P < 0.05$). They represented respectively 20% and 10% of the total number of plant-feeding nematodes. The lowest number of plant-feeding nematodes was found in macropore water (18 individuals per 100 g of unfractionated soil), A1000 (37 individuals per 100 g of unfractionated soil), and A200 (12 individuals per 100 g of unfractionated soil). Densities of plant-feeding nematodes were similar (about 10 individuals g^{-1} of habitat) in habitats A5000, A2000 and A1000 (Fig. 4). For the habitats A200 and A50, densities were respectively lower (2 individuals g^{-1} habitat) and much higher (38 individuals g^{-1} habitat).

The free-living nematodes comprised mainly Dorylaimidae and some rare Cephalobidae. They were principally recovered from habitats A50 (631 individuals per 100 g of unfractionated soil), A5000 (287 individuals per 100 g of unfractionated soil) and A2000 (159 individuals per 100 g of unfractionated soil). These amounts, representing 51%, 23% and 13% of the total number of free-living nematodes, were significantly higher than those measured in the other habitats. Free-living nematodes extracted from roots + rhizosphere were found only in the rhizosphere fraction. Macropore water and habitat A200 contained very few free-living nematodes (about 24 individuals per 100 g of unfractionated soil). Densities of free-living nematodes exhibited similar trends to those of plant-feeding nematodes. For habitat A50, the density of free-living nematodes was even higher than that of plant-parasitic nematodes (72 and 38 individuals per 100 g of unfractionated soil, respectively). However, this difference was not significant (Wilcoxon non-parametric test, $P < 0.05$), indicating that the distribution of plant-feeding and free-living nematodes within a habitat was not different, except for the roots and rhizosphere, where free-living nematodes were less abundant.

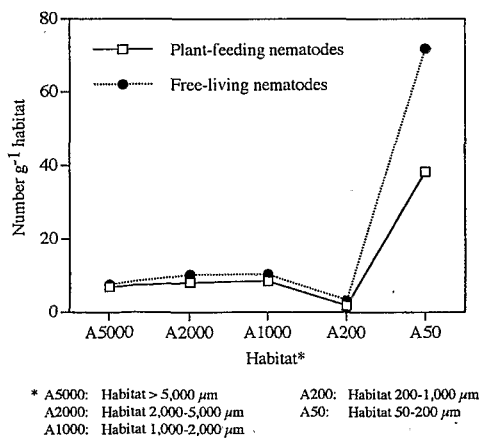


Fig. 4. Density of plant-feeding and free-living nematodes in the different habitats.

4. Discussion

4.1. Reliability of the fractionation method and characteristics of habitats A5000 and A2000

Physical fractionations have been used worldwide for many years. Most of these methods consist of dispersion and sieving procedures. Dispersion involves either chemical agents (Turchenek and Oades, 1979; Feller et al., 1991) or physical forces such as marbles (Brückert, 1979) or ultrasound (Tiessen and Stewart, 1983; Feller et al., 1991). However, soil aggregates and associated microorganisms are strongly altered during dispersion. Chotte et al. (1992) and Chotte et al. (1993) demonstrated that clay particles, recently immobilised ^{15}N and microorganisms originally associated with aggregates of 250–2000 µm were displaced to the clay fraction during dispersion using agate marbles. Therefore, they developed the so-called gentle method for soil fractionation (Chotte et al., 1994). This method, used here, allows full recovery of biomass C on soil fractionation. Moreover, it has been demonstrated to separate rhizospheric from non-rhizospheric aggre-

gates and preserve their organic and biological characteristics (Kabir et al., 1994), which indicates its reliability.

For this vertisol under pasture, habitats over 2000 μm (A5000 and A2000) accounted for more than 50% of the soil weight and 50% of organic carbon of the soil (Kabir et al., 1994). Morphological observations of these macroaggregates revealed that they consist of bacteria-sized aggregates and organic remnants coated in an abundant clay plasma entangled by thin roots (Chotte et al., 1994). This hierarchy in the soil aggregation process is consistent with the model described by Oades and Waters (1991). Spatial arrangements of these structures created intra-aggregate planar voids 150–50 μm wide.

4.2. Nematode soil habitats

The main plant-feeding nematodes recovered (*Pratylenchus zeae*, *Tylenchus* sp.) were broadly similar in body length (340–900 μm) and width (15–20 μm), except for the rarely encountered *Xiphinema setariae* (over 2000 μm). Other species from the free-living nematode community (mainly Dorylaimidae) were larger in body length (up to 3000 μm) and width (47 μm). Nematodes are distributed according to feeding habits and body size (Jones, 1982; Elliott et al., 1984). They inhabit permanently (e.g. free-living nematodes) or temporarily (e.g. some plant-feeding nematodes) water-filled pore space. According to these constraints, we can proposed three different categories, adapted from Beare et al. (1995), for nematodes habitats.

4.2.1. Roots and the rhizosphere

Roots represent the major food resource for plant-feeding nematodes. Accordingly, it was not surprising to find a high proportion (39%) of total plant-feeding nematodes confined to the roots (endoparasitic species) and the rhizosphere (ectoparasitic species). Plant-feeding nematodes would have been confined to the rhizosphere if the plant-feeding community had been dominated by ectoparasitic nematodes.

In contrast, free-living nematodes which preyed on bacteria or organic remnants were found exclusively in the rhizosphere but in very low quantities (5% of total free-living nematodes). No evidence was available to explain this result.

4.2.2. Porosphere

Compared with the model of Beare et al. (1995), the porosphere is defined as inter-aggregate pores, intra-aggregate pores being referred to as aggregatusphere.

Only very low proportions of the total numbers of plant-feeding (1%) and free-living (2%) nematodes were present in the macropore water (diameter over 300 μm). These values are based on the assumption that nematodes inhabiting a particular fraction were unlikely to have migrated during the fractionation procedure, as soil nematode migration is strongly restricted in clay soils (Wallace, 1971). This result accommodated the fact that nematodes do not occur in large pores as a pore size larger than the body width of a nematode greatly impedes its movements (Jones, 1982).

For the habitat 50–200 μm (A50), the numbers of plant-feeding and free-living nematodes per gram of habitat were much higher than those for the other habitats. However, the exact location of nematodes associated with this fraction is questionable because of their body size. If we assume that the average habitat of this size is a sphere 125 μm in diameter, it is unlikely that almost half of its volume would be occupied by one nematode (30 μm in diameter and 600 μm in length). Therefore, we can conclude that nematodes collected from this habitat on the 50 μm sieve actually resided within the inter-aggregate pores from 50 to 300 μm in diameter. Among these pores, those 50–150 μm in diameter are partly responsible for the higher soil porosity under pasture than under continuous crops (J.L. Chotte, unpublished data, 1995). A similar conclusion was drawn by Hassink et al. (1993) who indicated that pores 30–90 μm in diameter explained 84% of the variation in nematode biomass.

It can be concluded that 27% and 53% of the total numbers of plant-feeding and free-living nematodes, respectively, resided in inter-aggregate pores, most of them being located in pores 50–300 μm in diameter. These plant-feeding nematode may originate from roots present in the inter-aggregate pores or at the outer part of coarse aggregates (Chotte et al., 1994). The abundance of free-living nematodes is consistent with the presence of large amounts of bacteria in the dispersible clay fractions (Kabir et al., 1994). However, we can also hypothesise that the porosphere

corresponds to a transient niche, where nematodes migrate to their food sources, inter-aggregate pores offering more suitable space than intra-aggregate pores for nematode movement.

4.2.3. Aggregatusphere

Plant-feeding and free-living nematodes residing in the aggregatusphere (habitats A5000, A2000, A1000 and A200) represented 34% and 42%, respectively, of the total numbers of nematodes. Irrespective of their feeding habits, the numbers of plant-feeding and free-living nematodes per gram of habitat were similar and constant (10 individuals g^{-1} of habitat) for habitats coarser than 1000 μm (A5000, A2000, A1000). Irrespective of whether the food resource was roots or bacteria, they were uniformly distributed within habitats. These habitats were therefore colonised by nematodes to the same extent. In contrast, the densities of plant-feeding and free-living nematodes decreased sharply in the finest habitats (A200). These habitats may not offer suitable amounts of food, as suggested by morphological observations indicating that roots are more likely to be found in larger aggregates (Chotte et al., 1994). However, this view is weakened by the fact that the density of bacteria, the main food resource for free-living nematodes, did not demonstrate a similar trend (Kabir et al., 1994). The lower density of nematodes within the habitat 200–1000 μm may have arisen because of physical constraints, nematodes being too large to reside in this habitat.

This gentle physical method used to fractionate the soil provided us with useful indications about the distribution of nematodes in this highly aggregated vertisol under pasture. Feeding habits and physical constraints of soil habitats were the main factors responsible for the distribution of plant-feeding and free-living nematodes within soil habitat, roots + rhizosphere, inter-aggregate pores and coarser habitat being the sites most conducive for nematodes colonisation. The distribution of free-living nematodes differed from their food resource; thus, they may be used as a bio-indicator of soil physical constraints.

Acknowledgements

The authors would like to thank Dr. Adrian Harris (CSIRO, Div. of Soil) for carefully reading the manuscript and are grateful to anonymous reviewers for their helpful comments.

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Reprinted from

Applied Soil Ecology

A section of Agriculture, Ecosystems & Environment

Applied Soil Ecology 4 (1996) 193–200

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Accepted 13 May 1996