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DIVERSITY, STRUCTURE, AND EVOLUTION OF FUNGAL COMMUNITIES IN SOILS UNDER DIFFERENT AGRICULTURAL MANAGEMENT PRACTICES

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Summary: This work investigates the diversity, structure and evolution of fungal communities in soils, which have been recently subjected to agricultural practices. The soils analyzed belong to two different management regimens in the El Salado river basin (Buenos Aires, Argentina). An attempt is made to analyze the sustainability of continuous crop rotation (soil I) and crop-pasture rotation (soil II) under conventional or no-tillage managements. Three groups of fungi were delineated based on frequency patterns: dominant, opportunist and specialist. Rank-frequency diagrams show that the fungal diversity (richness and evenness) increases immediately in response to tillage and cultivation (soybean, wheat) or mixed-legume-grass pasture production. The results obtained point out the existence of a strong fungal association, irrespective of the agronomic and management practices.

Key words: fungal diversity, evenness, richness, conventional or no-tillage, sustainability.

Resumen: Diversidad, estructura y evolución de comunidades fúngicas en suelos sometidos a diferentes prácticas agrícolas. Este trabajo investiga la diversidad, estructura y evolución, de las comunidades fúngicas en suelos recientemente sujetos a la agricultura. Los suelos analizados corresponden a dos experimentos diferentes en la depresión del río El Salado (Buenos Aires, Argentina) y se procura analizar la sustentabilidad de rotaciones continuas de cultivos (Suelo I) y rotaciones de cultivo-pastoreo (Suelo II) bajo manejos convencionales y siembra directa. Se agruparon a las especies fúngicas, de acuerdo a patrones de frecuencias, en tres grupos: dominantes, oportunistas y especialistas. Los diagramas de rangos de frecuencia muestran que la diversidad fúngica (riqueza y regularidad) aumenta inmediatamente en respuesta a la labranza y al cultivo de soja, trigo o pasturas mixtas de leguminosas y gramíneas. Los resultados obtenidos señalan la existencia firme de una asociación fúngica independiente de las prácticas agronómicas y de los manejos estudiados.

Palabras clave: diversidad fúngica, regularidad, riqueza, labranza convencional, siembra directa sustentabilidad.

INTRODUCTION

Microorganisms respond integrally and sensitively to soil environment (Ahmad & Baker, 1987; Alexander, 1991; Stenberg, 1999) thus therefore they may be used to assess the effect of perturbations (O'Donnell *et al.,* 1996; Kennedy & Gewin, 1997; Calderon *et al*., 2000).

Soil microbial biomass comprises 1% to 4% of the total organic carbon (Anderson & Domsch 1985), and 2% to 6% of the total organic nitrogen (Jenkinson 1988) in soil. Microorganisms play the crucial role of maintaining nutrient cycles in soil (C, N, P, S) through recycling of organic matter. The latter is fundamental, not only for primary production, but for the long-term functioning of ecosystems (Stevenson, 1986; Doran & Parkin, 1994, 1996) and justifies estimation of microbial biomass and respiration in any set of data for the assessment of soil quality (Doran & Parkin, 1994; Turco *et al.,* 1994; Stenberg, 1999; Aon & Colaneri, 2001; Aon *et al*., 2001b, c; Cortassa *et al.,* 2001).

Fungi often make up at least 75% to 95% of the soil microbial biomass, and together with bacteria, are responsible for about 90% of the total energy flux of organic matter decomposition in soil (Carlile & Watkinson, 1994). Our previous data showed that fungal biomass was higher 10-30:1 with respect to

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bacterial biomass in soils from the El Salado river basin (Buenos Aires, Argentina) (Aon *et al.*, 2001a, b, c) based on culture-dependent (plate counting) and -independent (lipid markers, enzymatic) methods used for soil fungal biomass estimation (Gaspar *et al.* 2001). Similar biomass ranges for bacteria, i.e. 20-80 or 50-80 kg biomass ha^{-1}, were determined in the two soils from the El Salado river basin analyzed in the present work. However, these two soils differed widely in fungal biomass, i.e. 100-800 or 500-2000 kg biomass ha^{-1}, respectively (Aon *et al.* 2001a, c; Gaspar *et al.* 2001). We found a 16% increase in the biodiversity of fungi during a soybean crop in a soil recently subjected to agriculture (Aon *et al.* 2001a).

We attempted to characterize the soil diversity, structure and evolution of the fungal community from two soils recently subjected to tillage and crop production. These two soils from the El Salado river basin (Buenos Aires, Argentina) corresponded to different long-term experiments attempting to analyze the sustainability of continuous crop and pasture-crop rotations under conventional or no-till managements.

Materials and Methods

Soil characteristics, experimental design, and sampling procedure

The soils examined (soil I: Aquid Argiudoll, and soil II: Hapludol) in the "El Salado" river basin (central eastern of the province of Buenos Aires, Argentina) present high organic carbon (OC) contents, low phosphorus, and acid pH, corresponding to natural grass lands that were conventionally managed only two to four years before present experiments (soil I: 1998; soil II: 1996) (Aon *et al.*, 2001a; Aon & Colaneri, 2001).

Conventional tillage (CT) was compared to no-till (NT) management under a continuous crop rotation (soybean, wheat) (soil I) (Aon *et al.*, 2001a) or a crop-pasture rotation consisting of corn (*Zea mays* L.) and a mixed-grass-legume pasture (soil II) (Aon *et al.*, 2001b, c). The mixed-legume-grass pasture in soil II comprised the following plant species: *Dactylis glomerata* cv. Porto (3 kg seeds ha^{-1}); *Phalaris tuberosa* cv. El Gaucho (5 kg seeds ha^{-1}); *Bromus unioloides* cv. Martín Fierro (5 kg seeds ha^{-1}); *Lolium perenne* cv. Grasslands Nui (2.5kg seeds ha^{-1}); *Trifolium repens* cv. El Lucero (1.5 kg seeds ha^{-1}); *Trifolium pratense* cv. Quiñequelli (2 kg seeds ha^{-1}); *Lotus corniculatus* (3 kg seeds ha^{-1}).

Treatments (NT or CT) were arranged in a randomized, complete block design, and replicated four times (soil I) or in a randomized, split plot design, replicated four times with split for nitrogen fertilization (diammonium phosphate, 18-46-0: 79 kg ha^{-1}) at the beginning of the pasture planting (soil II).

The initial status of soil I corresponds to the sampling before plowing and seeding soybean during 1998, while the initial status of soil II belongs to a soil that was uncultivated for at least 20 years with respect to crop-pasture rotation plots. The sampling schedule of soil I was the following: 1998 soybean (pre-harvest); 1999 and 2000 wheat (middle growth cycle); and that corresponding to soil II was: 1998 to 2000 mixed-pasture (sampling time: November).

In the present work, fungi were monitored in the top soil profile: 0-5 cm or 5-10 cm as indicated in each case, at different stages of soybean [*Glycine max* (L.) Merr.], or wheat [*Triticum aestivum* L.] crops growth in soil I, or mixed-legume-grass-pasture (soil II). We did a composite random (i.e. serpentine, Dick *et al.*, 1996) sampling method distributed in row and inter-row locations. Soil samples were collected for test by using a 20 mm (i.d.) hand probe to a depth of 20 cm. The soil column corresponding to the 0-5 cm or 5-10 cm depth, was directly stripped from the hand probe. At the places where each sample was collected, we pooled 5 to 6 sub-samples from a square of *ca.* 3 m^2.

Fungal identification

The soil washing method described in Parkinson & Williams (1961) was utilized to observe living fungi species as described in Gaspar *et al.*, (2001). Briefly, eighty to one hundred soil particles were plated in malt agar (20 g/L) with glucose (20g/L) in the presence of 0,5g/L streptomycin sulfate and 0,25g/L chloramphenicol at a rate of four particles per plate. Petri plates (9mm d) were incubated at 25°C and observed microscopically at one-week interval. Original taxonomic papers and Domsch *et al.*, (1993) were used for identifying sporulating fungi. The relative percentage of occurrence for each fungi species was calculated as: (number of particles bearing a specified fungus / total number of particles) x 100 (Godeas, 1983).

Estimation of fungal taxonomic diversity

Fungal species growing from soil particles, were observed and their relative percentage of frequency quantified; their contribution to diversity was used to calculate a biodiversity index (Shannon-Weaver), *H*. Species richness, *S*; and evenness, *E*, were also quantified (Magurran, 1988).

The Shannon-Weaver index, *H*, of biodiversity measures the amount of «information» (in bits) contributed by each individual across the total population observed (see Tables 1, 2) (Frontier & Pichod-Viale, 1995). The sum of the individual contributions $\sum (-p_i \log_2 p_i)$ gives H. The maximal contribution per individual species is 0.53 bits when its probability of appearance, p_i, is close to 0.37 (Frontier & Pichod-Viale, 1995). We arbitrarily defined $(-p_i \log_2 p_i)$ high (> 0.4), intermediate ($0.17 < (-p_i \log_2 p_i) < 0.4$), and low ($< 0.17$).

RESULTS

The species of fungi present in soil were taxonomically identified, and their relative percentage as well as contribution to quantified diversity. The main results obtained are shown in Tables 1, 2. The responsiveness of the fungal species and population to management in soils I and II, and the changes of the community structure, were assessed through quantification of their relative percentage in rank-frequency diagrams (Figs. 1, 2) and contribution to global taxonomic diversity by individual species (Tables 1, 2).

Evolution of the fungal community structure and estimation of fungal diversity

Rank-frequency diagrams (RFD) represent a useful tool for quantitatively depicting the structure of microbial communities (Frontier & Pichod-Viale, 1995). The shape of the RFD changes as a function of the specific diversity giving a global representation of diversity, *H*. The two main components of *H*, i.e. the number of species, *S*, and the evenness, *E*, can be easily appreciated in the RFD. In fact, *S* is given by the curve extension to the right while *E* denotes the concave or convex shape of the plot. Otherwise, a

Table 1. Contribution of each species from the fungal community present in soil (continuous crop rotation) to the total fungal biodiversity during a three-yr sampling period respect to an initial status (natural grassland) in the El Salado river basin (Buenos Aires, Argentina). Species are ordered according to their contribution to the biodiversity index *(H)*. Key to abbreviations: n.d., not detected; NT, no-tillage; CT, conventional tillage; *H*, biodiversity index (Shannon-Weaver); *S*, species richness; *E*, evenness.

Fungal species	Initial status	1998 (soybean)		1999 (wheat)		2000 (wheat)	
		CT	NT	CT	NT	CT	NT
Fusarium oxysporum	0.52	0.43	0.53	0.515	0.52	0.53	0.53
Trichoderma koningii	0.52	0.48	0.42	0.40	0.345	0.50	0.45
Zygorrhynchus moelleri	0.28	0.22	0.41	0.32	0.29	0.41	0.44
Trichoderma saturnisporum	0.18	0.32	0.245	0.47	0.46	0.23	0.07
Gliocladium roseum	0.375	0.14	0.08	0.09	0.21	0.13	0.07
Fusarium solani	0.18	0.095	0.06	0.19	0.29	0.27	0.215
Penicillium rubrum	0.21	0.25	0.24	0.21	0.16	0.24	0.23
Penicillium thomii	0.14	0.485	0.325	0.14	0.21	0.09	0.19
Humicola fusco-atra	0.08	0.15	0.165	0.15	0.14	0.07	0.19
Aspergillus fumigatus	0.13	0.1	0.06	n.d.	n.d.	n.d.	n.d.
Mucor hiemalis	0.08	0.06	n.d.	n.d.	n.d.	n.d.	0.07
Aspergillus terreus	0.08	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Gongronella butleri		0.07	0.03	n.d.	0.04	0.05	0.09
Penicillium restrictum		0.11	0.08	n.d.	0.07	n.d.	n.d.
Dematiaceous sterile mycelium		0.05	n.d.	n.d.	n.d.	n.d.	n.d.
Talaromyces helicus		0.14	0.06	n.d.	0.04	n.d.	n.d.
Thielavia basicola		0.11	0.06	n.d.	n.d.	n.d.	n.d.
Trichoderma harzianum		n.d.	0.03	0.24	0.21	n.d.	n.d.
Myrothecium verrucaria		n.d.	0.06	n.d.	n.d.	n.d.	n.d.
Penicillium megasporum		n.d.	0.03	n.d.	n.d.	n.d.	n.d.
Rhizopus stolonifer		n.d.	0.1	n.d.	n.d.	n.d.	n.d.
Paecilomyces lilacinum		n.d.	n.d.	0.035	n.d.	0.03	0.1
Cylindrocarpon didymum		n.d.	n.d.	0.06	0.07	0.03	n.d.
Chaetomium globosum		n.d.	n.d.	0.04	n.d.	n.d.	n.d.
Mortierella sp.		n.d.	n.d.	n.d.	0.095	0.53	0.09
Cylindrocarpon obtusisporum		n.d.	n.d.	n.d.	0.04	n.d.	n.d.
Hyaline sterile mycelium		n.d.	n.d.	n.d.	n.d.	0.03	n.d.
Aspergillus flavus		n.d.	n.d.	n.d.	n.d.	0.03	n.d.
Nigrospora sphaerica		n.d.	n.d.	n.d.	n.d.	n.d.	0.03
Rhizoctonia sp.		n.d.	n.d.	n.d.	n.d.	n.d.	0.03
H	2.775	3.21	2.985	2.86	3.19	3.17	2.785
S	12	16	18	13	16	15	15
E	0.77	0.8	0.72	0.77	0.8	0.81	0.71

Table 2. Contribution of each species from the fungal community present in soil (crop-pasture rotation) to the total fungal biodiversity during a three-yr sampling period respect to an initial status (at least 20 yr of any labor) in the El Salado river basin (Buenos Aires, Argentina). Species are ordered according to their contribution to the biodiversity index *(H)*. Key to abbreviations: see Table 1.

Fungal species	Initial status	1998 (mixed-pasture)		1999 (mixed-pasture)		2000 (mixed-pasture)	
		NT	CT	NT	CT	NT	CT
Fusarium oxysporum	0.53	0.44	0.365	0.27	0.48	0.53	0.52
Penicillium rubrum	0.05	0.31	0.26	0.33	0.26	0.15	0.27
Trichoderma koningii	0.42	0.39	0.34	0.50	0.525	0.52	0.48
Trichoderma saturnisporum	0.4	0.43	0.47	0.25	n.d.	0.28	0.18
Fusarium solani	0.16	0.13	0.14	n.d.	0.065	0.19	0.14
Gliocladium roseum	0.38	0.215	0.14	n.d.	0.27	0.03	0.05
Zygorrhynchus moelleri	0.33	0.31	0.14	n.d.	n.d.	0.22	0.25
Humicola fusco-atra	0.11	0.25	0.14	n.d.	n.d.	0.06	0.17
Absidia spinosa	0.065	n.d.	n.d.	n.d.	n.d.	0.035	n.d.
Epicoccum purpurascens	0.03	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Penicillium thomii		0.33	0.40	0.37	0.29	0.25	0.34
Aspergillus fumigatus		0.33	0.385	n.d.	0.16	0.09	0.22
Aureobasidium pullulans		0.08	n.d.	n.d.	n.d.	n.d.	n.d.
Aspergillus niger		n.d.	0.185	0.12	n.d.	n.d.	0.05
Talaromyces helicus		n.d.	0.14	n.d.	0.065	n.d.	n.d.
Aspergillus terreus		n.d.	0.08	n.d.	n.d.	n.d.	n.d.
Cylindrocarpon didymum		n.d.	0.08	n.d.	n.d.	n.d.	n.d.
Mucor mucedo		n.d.	0.08	n.d.	n.d.	n.d.	n.d.
Verticillium psalliotae		n.d.	0.08	n.d.	n.d.	n.d.	n.d.
Mucor hiemalis		n.d.	n.d.	0.06	n.d.	0.035	n.d.
Gongronella butleri		n.d.	n.d.	n.d.	0.19	0.07	0.19
Arthrinium phaeospermum		n.d.	n.d.	n.d.	0.065	n.d.	0.03
Gonythrichum macrocladum		n.d.	n.d.	n.d.	0.07	n.d.	n.d.
Paecilomyces lilacinus		n.d.	n.d.	n.d.	0.065	n.d.	n.d.
Rhizopus stolonifer		n.d.	n.d.	n.d.	0.065	n.d.	n.d.
Cladosporium sphaerospermum		n.d.	n.d.	n.d.	n.d.	0.03	0.03
Aspergillus flavus		n.d.	n.d.	n.d.	n.d.	0.05	n.d.
Mortierella sp.		n.d.	n.d.	n.d.	n.d.	n.d.	0.07
Dematiaceous sterile mycelium		n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
H	2.475	3.215	3.425	1.9	2.57	2.57	2.99
S	10	11	16	7	13	15	15
E	0.74	0.93	0.86	0.68	0.69	0.66	0.77

small number of abundant species together with a few less frequent ones imply weak *H* and *E* characterized by a concave diagram. On the other hand, convex diagrams are indicative of an important number of species of relatively high frequency but without dominant ones, and a group of species with low frequency, i.e. high *H* and *E*.

The initial status of the fungal community structure in soils I and II is shown in Figures 1 and 2. In the case of soil I the concave shape of the RFD indicates a mature fungal community (Fig. 1A) with H=2.775; S=12, and E=0.77 (Table 1). This is also reflected by the contribution to diversity by each of the species of the fungal community shown in Table 1, i.e. a small number of abundant species together with a few less frequent ones. In contrast, soil II shows a community dominated by a few predominant species accompanied by a group of species with low frequency (Fig. 2A; Table 2).

Ecologically speaking, young systems are characterized by a concave RFD with greater number of species. Diversity and evenness increase in both soils as can be judged through the convex shape of the plots (Figs. 1 B-D, 2 B-D). As ecosystems become complex, the RFD becomes convex. Diversity readjustment after a transient increase is reflected by the appearance of straight portions in the RFDs (see Figs. 1C, 2 C).

Characterization of the fungal community

The analysis of the fungal community in the two soils from the El Salado river basin allowed us to identify at least three groups, on the basis of their contribution to diversity *(i)* dominant, that behave as resident species with high frequency of appearance (see M&M for definition of high, intermediate and low frequencies); *(ii)* opportunist, that appear occasionally with lower frequency than the dominant group; *(iii)* specialist, that appear under a combination of specific conditions (e.g. crop, management and soil water content).

Within the group of dominant species, *Fusarium oxysporum*, *F. solani*, *Trichoderma koningii*, *Penicillium rubrum*, *Gliocladium roseum*, *T.*

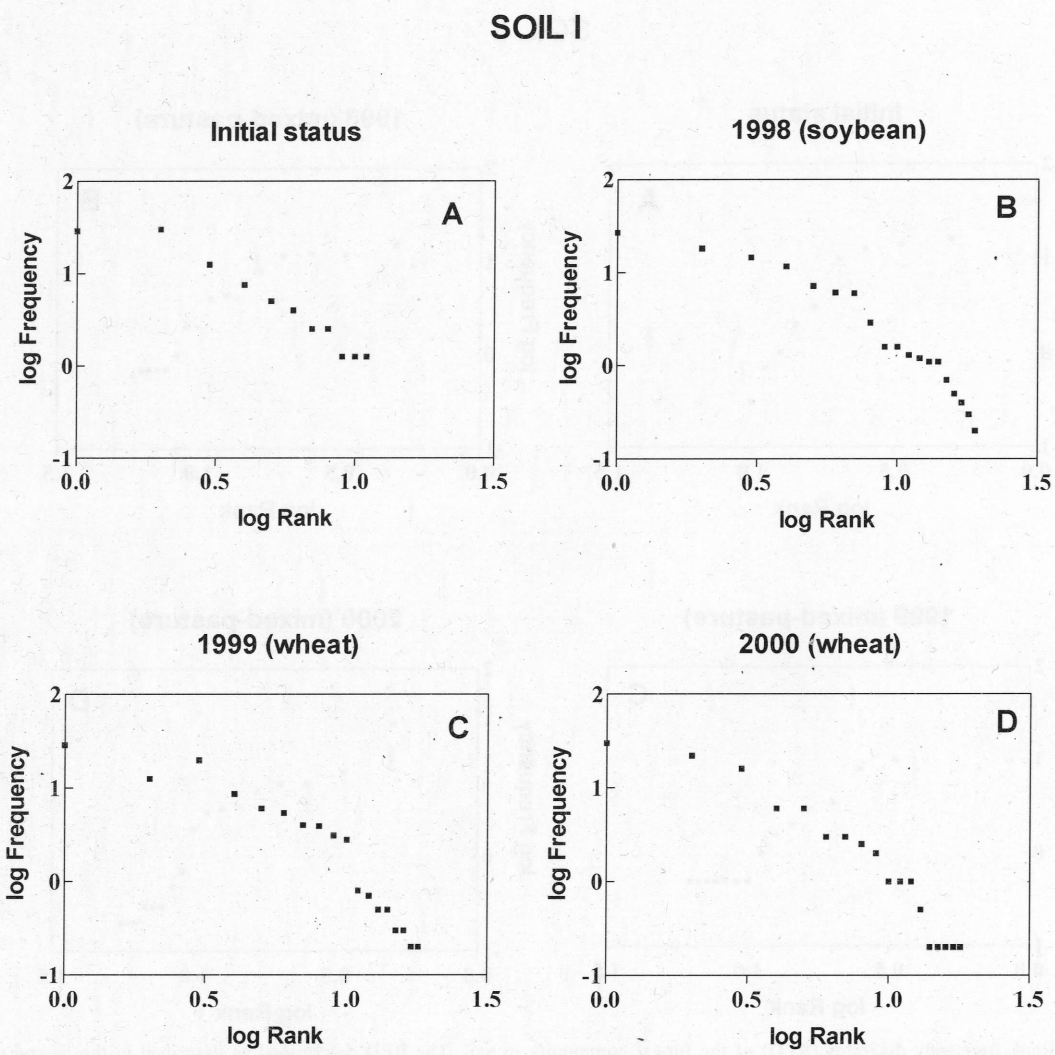

Fig. 1. Rank-frequency diagrams (RFD) of the fungal community in soil. The RFD is, essentially, a double log plot in which the *x*-axis is the log of the rank of each fungi species classified with successive integers (i.e. 1, 2, 3...,) according to their abundance whereas the *y*-axis corresponds to the log of the relative contribution (in percentage) of each species in the whole collection determined. Shown in panels A-D are the data belonging to the initial soil status, and the 1998-2000 sampling times, respectively, as indicated (see also M&M).

saturnisporum and *Zygorrhynchus moelleri* appeared in nearly all sampling times during the three years in both soils (Tables 1 and 2). Moreover, the first four species of this group were detected also in natural grasslands from the El Salado river basin confirming their widespread distribution in these soils (Cabello & Aon, unpublished results).

All the species of fungi, except *Z. moelleri* from the dominant group, have been characterized as cellulose decomposers; some of which are very active (*Trichoderma koningii*, *Gliocladium roseum*) (Domsch *et al.*, 1993). *Penicillium thomii* and *Humicola fusco-atra* belong to the group of dominant species referred above (Tables 1 and 2).

Aspergillus fumigatus, Myrothecium verrucaria, *Penicillium megasporum*, *Rhizopus stolonifer* and *Thielavia basicola* or *Chaetomium globosum, Cylindrocarpon obtusisporum, A. flavus*, *Nigrospora sphaerica* and *Rhizoctonia* sp. belong to the opportunists group in soil I during soybean or wheat crops, respectively (Table 1).

Specialist fungi such as *Paecilomyces lilacinus*, *Cylindrocarpon didymum* and *Mortierella* sp. were detected in wheat crops from the same soil during two consecutive years (1999-2000, Table 1).

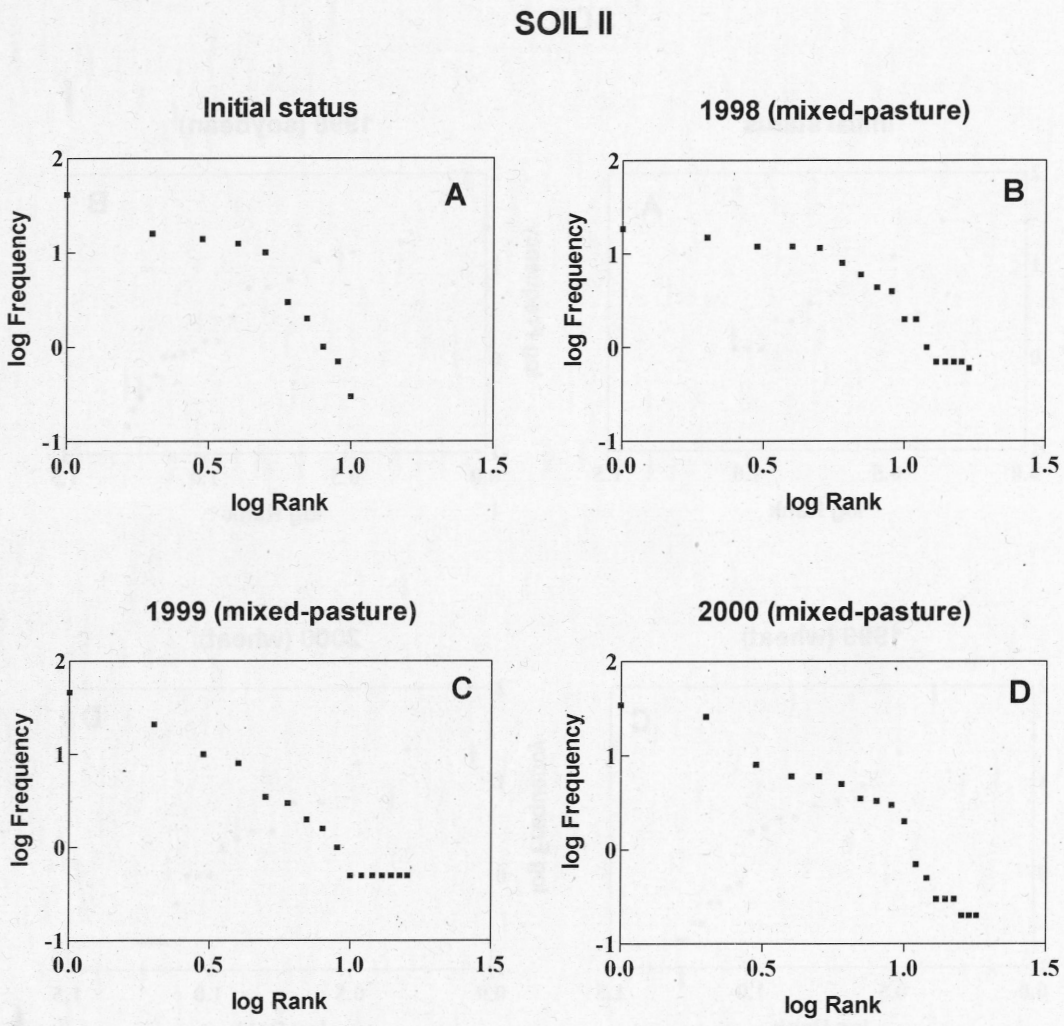

Fig. 2. Rank-frequency diagrams (RFD) of the fungal community in soil. The RFD determined as described in the legend of Figure 1, is shown in panels A-D for the initial soil status and the 1998-2000 sampling times, respectively.

In soil II, opportunist fungi in either conventional- or no-tillage were *A. niger*, *Gongronella butleri* and *Cladosporium sphaerospermum*. In the same soil, specialist fungi were detected under conventional tillage (*Arthrinium phaeospermum*, *Aspergillus terreus*, *Cylindrocarpon didymum*, *Mucor mucedo*, *Verticillium psalliotae*, *Gonythrichum macrocladum*, *P. lilacinus*, *R. stolonifer*, *Talaromyces helicus*) or no tillage (*A. flavus*, *M. hiemalis*, *Mortierella* sp.) (Table 2).

Similar distribution (in percentage) of species within the main classes of fungi were determined in soils I and II, respectively: Zygomycetes (18% and 24%), Ascomycetes (9% and 7%), and anamorphs of Ascomycetes (73% and 69%).

An important finding is that the group of dominant species does not account for the differences in *H* and *E* found in favor of soil I with respect to soil II (except for the 1999 sampling; compare Tables 1 and 2) but the groups of opportunists and specialists. The appearance and disappearance of species from the latter groups more likely reflect annual differences arising from the combination of physico-chemical properties, management, and climate (e.g. rainfall).

Discussion

We systematically monitored (1998-2000) and compared to an initial soil status (Aon & Colaneri, 2001; Aon *et al.*, 2001a, b, c) for 3 years.

The diversity of the fungal community, both in richness and evenness, readily increased in response to soil tillage either under continuous crop rotation

or crop-pasture rotation. In the 1999 sampling, fungal biomass decreased 3- to 4 fold in soil II compared to soil I, but displayed two- to three-fold higher respiration rates (in kg O_2 or kg CO_2-C per ha per day) (Aon & Colaneri, 2001; Aon *et al.*, 2001a, b, c). Moreover, the diversity index was much higher in soil I than II independent of management regime (compare Tables 1 and 2, 5th and 6th columns). This observation is consistent with the notion that the heterogeneity and abundance of a fungal community is not always correlated with the metabolic activity of that community (Kennedy & Gewin, 1997). In fact, the lower amounts and diversity of the fungal community in soil II correlated with a higher activity as measured by soil respiration (Aon *et al.*, 2001c).

A main conclusion of the present work shows that a specific pattern of dominant species from a group of strongly associated fungi exists in both soils irrespective of management practice. Probably, the strong fungal association existing within the dominant group reflects not only a response to the soil environment but also complex biotic interactions between classes (Anamorphs, Ascomycetes, Zygomycetes) and species. Indeed, the structure, evolution and diversity, of the fungal community detected in soils from the El Salado river basin suggest complex biotic interactions. The three main groups of dominant, specialist and opportunist species proposed, include primary and secondary saprotrophic colonizers as well as members of the genera

Trichoderma and *Fusarium* that can act as antagonists of soil borne plant diseases (Ahmad & Baker 1987) or plant vascular pathogens (Onyike & Nelson 1993), respectively.

The strong fungal association belonging to the group of dominant species likely represents a microbial pattern that in turn mirrors a specific pattern of interactions between microbial, physical, chemical and biochemical properties (Aon & Colaneri 2001; Aon *et al.* 2001a). This fungal association might characterize important functions (e.g. nutrient cycling) related with soil quality in the El Salado river basin, because the pattern is consistent among different agronomic schemes and management, and in natural grasslands.

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