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Population dynamics of *Monosporascus cannonballus* ascospores in marsh soils in eastern Spain

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Abstract

The population dynamics of *Monosporascus cannonballus* ascospores in the soils of four muskmelon fields located in a marsh area in Castellón province (eastern Spain) was studied for a 3 year period. Two of these fields were cropped to muskmelon with fallow periods between muskmelon cropping, and the others were in fallow and had extensive flooding periods. Muskmelon cultivation resulted in a progressive increase of the number of ascospores in soil, reaching a maximum 7 months after muskmelon planting (2–4 months after plant death), and a subsequent decline during fallow periods between muskmelon crops. During muskmelon cropping, in-bed and between-bed ascospore numbers were compared and, in general, there were no statistical differences between them. In the fields which were in fallow and flooded, the dynamics found was a progressive decline of the population of ascospores. Soilborne inoculum was viable and capable of infecting muskmelon at the end of the 3 year period in all fields, demonstrating that ascospores of *M. cannonballus* are able to survive for this period of time in the absence of muskmelon cultivation and also that this fungus seems to be well adapted to survive in soils which maintain a high water table during the crop or under flooding conditions.

Introduction

Monosporascus root rot/vine decline, caused by the soilborne ascomycete *Monosporascus cannonballus* is a destructive disease of muskmelon (*Cucumis melo*) and watermelon (*Citrullus lanatus*) worldwide (Martyn and Miller, 1996; Cohen et al., 2000). Symptoms of this disease include yellowing and death of the crown leaves and a gradual decline of the vine as the plant approaches maturity. Root systems become necrotic, with numerous discrete lesions and lack most of the secondary and tertiary feeder roots (Martyn and Miller, 1996). Characteristic perithecia of the fungus are formed in the cortex of colonized roots, which produce large numbers of distinctive, spherical, thick-walled ascospores (Martyn and Miller, 1996; Stanghellini et al., 1996). These ascospores can be detected and quantified in the soil by a physical extraction method based on a sucrose centrifugation technique (Stanghellini and Rasmussen, 1992; Mertely et al., 1993b).

In Spain, *M. cannonballus* was first reported in muskmelon fields in 1989 (Lobo-Ruano, 1990). The incidence of this pathogen increased progressively (García-Jiménez et al., 1993) and, in surveys conducted from 1994 to 1996, *M. cannonballus* was isolated from 68.4% of the muskmelon fields showing symptoms of vine decline (García-Jiménez et al., 2000). At present, *M. cannonballus* is widespread in most of the Spanish muskmelon production areas, where it can be isolated from

diseased roots, sometimes associated to other soil-borne vine decline fungal pathogens such as *Acremonium cucurbitacearum* and *Rhizopycnis vagum* (Alfaro-García et al., 1996; García-Jiménez et al., 2000; Armengol et al., 2003).

Monosporascus cannonballus has a severe impact on spring–summer muskmelon crops in areas of marsh soils in Castellón province (eastern Spain), which maintain a high water table during cropping season and are often flooded for several months each year during winter months (García-Jiménez et al., 1993, 2000). This is in contrast with the presumed natural habitats of this pathogen because the presence of *M. cannonballus* is characteristic of hot, arid and semi-arid melon-growing regions of the world (Martyn and Miller, 1996; Bruton et al., 1999; Pivonia et al., 2002) such as Tunisia (Martyn et al., 1994), the Lower Rio Grande Valley in Texas (Martyn and Miller, 1996), Saudi Arabia (Karlatti et al., 1997) and the Arava valley in Israel (Cohen et al., 2000). In addition, *M. cannonballus* is a high temperature fungus, with a growth optimum between 30 and 35 °C, which has been isolated from native desert (Sonora Desert) soils in Arizona (Stanghellini et al., 1996). One isolate from Libya was also reported to have a growth temperature optimum of 45 °C (Hawksworth and Ciccarone, 1978).

The objective of this work was to study the population dynamics of *M. cannonballus* ascospores in commercial muskmelon fields located in a marsh area at Castellón province during a 3 year period. Additionally, the effect of fallow and soil flooding on population densities and ascospore viability was examined.

Materials and methods

Experimental fields

Soil samples were collected monthly in four fields (fields A, B, C and D) located in Almenara (Castellón) for a 3 year period from July of 1999 to June of 2002. These fields are drip irrigated and can be flooded voluntarily by the growers. In this area, the soil has been classified as Gleysol (Rubio et al., 1995; F.A.O., 1998) and the texture was loam in the four fields. Soil pH was 7.92 for fields A and B and 8.02 for fields C and D. Fields B, C and D were cropped to cucurbits (mostly muskmelon) during each of the previous 3 years. Field A also was cropped to cucurbits except in 1998 when tomatoes were grown. Muskmelon and watermelon cultivars used in this area are: cv. Sancho (Piel de Sapo type) and cv. Dulce Maravilla respectively; both are susceptible to *M. cannonballus* (personal observations). In fact, the evaluation of these cucurbit crops in the previous years allowed the observation of symptoms of Monosporascus root rot/vine decline, which were confirmed by the isolation of the pathogen (data not shown).

Detailed cropping histories of these fields are presented in Table 1. During the period of study, field A was cropped to muskmelon in 1999 and 2001, and was in fallow in 2000 and 2002. Field B was cropped to muskmelon in 1999 and 2000, and was in fallow in 2001 and 2002. Planting and the end of the harvest dates are indicated in Table 1. Fields C and D were in fallow during the 3 years of study and had extensive flooding periods.

Table 1. Crop history in fields A, B, C and D, and crop sequence, fallow or flooding during the period of study

Year	Field A	Field B	Field C	Field D
1996	W[a]	W	M	W
1997	M	M	M	M
1998	T	M	M	M
Period of study				
1999	M (May–Sep)[b]	M (May–Sep)	Fl (Nov–Dec)	Fl (Nov–Dec)
2000	Fa	M (Jul–Sep)	Fl (Jan–Mar) (Oct–Dec)	Fl (Jan–Mar) (Oct–Dec)
2001	M (Jun–Sep)	Fa	Fl (Jan–Mar) (Oct–Dec)	Fl (Jan–Mar) (Oct–Dec)
2002	Fa	Fa	Fl (Jan–Jul)	Fl (Jan–Jul)

[a]Letters indicate the crops (M = muskmelon; T = tomato; W = watermelon) and fallow or flooding (Fa = fallow; Fl = flooding) in each field.
[b]Months in brackets indicate the duration of muskmelon crops from planting to the end of harvest, or flooding periods.

Soil sampling and processing

In fields A and B, which were already cropped to muskmelon when the study started in July of 1999, an area of approximately 8 m (four beds) in width and 3 m in length was chosen. In this area, nine soil samples were taken adjacent to the row of plants in the up-raised beds (in-bed) and nine samples from depressed areas between beds (between-bed), for a total of 18 samples. Samples of approximately 100 g were taken at 1 m intervals with a soil probe at 10–20 cm depth, which contains the highest population of ascospores (Mertely et al., 1993b). This sampling pattern was also adopted for fields C and D, which were in fallow in July of 1999, and maintained for the four fields in the same location during the period of study, even when they were flooded or in fallow.

Soil samples were air-dried at room temperature and sifted through a 2 mm sieve to remove soil clods prior to processing. Ascospores of *M. cannonballus* were extracted by a method adapted from Stanghellini and Rasmussen (1992). Each sample was passed through a 250 μm sieve. A 20 g subsample was mixed with 200 ml water, agitated on a magnetic stirrer for 5 min, and washed through nested 75 and 30 μm sieves. The material retained on the 30 μm sieve was centrifuged at 2000 *g* for 4 min. The supernatant was discarded and the pellet was resuspended in 30–40 ml of 50% sucrose and centrifuged for 2 min at 2000 *g*. Ascospores and other materials floating or suspended in the sucrose were decanted onto the 30 μm sieve and washed into a clean centrifuge tube. A second sucrose extraction was performed on the residual soil pellet to salvage spores not recovered during the first extraction. The resulting suspension from the second extraction was added to the first, and the combined suspension was stored in a small quantity of water at 4 °C until analyzed. Characteristic ascospores were enumerated in the water under a stereomicroscope at a magnification of 60×.

Bioassay of M. cannonballus *from soil samples*

The survival of *M. cannonballus* was verified for all fields at the end of the 3 year period using soil samples taken from March to June of 2002. In these months, soil from each field was used to fill plastic pots (14 cm diameter). Six pots per month and field were used to evaluate the ability of ascopores to infect seedlings through the reisolation of *M. cannonballus* from bioassay plants. Muskmelon seeds cv. Piel de Sapo PS-1430 were surface-disinfested in sodium hypochlorite (1.5% active chlorine) for 1 min, sown, and subsequently thinned to one seedling per pot. Plants were grown in a temperature-controlled greenhouse (25–30 °C), and fertilizer added twice during the experimental period using 150 ml per pot of Hoagland solution. Pots were arranged in a complete randomized design.

After 45 days, roots of each plant were exposed by carefully washing the soil away. For isolation, root fragments were surface sterilized for 1 min in a sodium hypochlorite solution (1.5% active chlorine) and washed twice with sterile water. Fourteen root segments per plant from apparently affected areas of tissue were transferred to potato dextrose agar (PDA) containing 0.5 mg ml^{-1} streptomycin sulphate (PDAS). Plates were examined daily for fungal growth for 7 days, and hyphal tips from all colonies were transferred to PDA for subsequent growth and sporulation.

Data analyses

Data were analysed using the software Statgraphics Plus 5.1 (Manugistics Inc., Rockville, MD, USA). The counts of the 18 soil samples from each field were averaged to obtain the monthly mean ascospore population. Analysis of variance (ANOVA) was conducted on these data. Regression analyses were performed to show the relationship between mean ascospore numbers per gram of soil and temporal variables during the period of study. Additionally, within the periods in which muskmelon was cultivated in fields A and B, ascospore count data were subjected to ANOVA to compare monthly in-bed and between-bed ascospore populations. Following ANOVA, mean comparisons were made using Tukey's multiple range test ($P < 0.05$).

Results

Population dynamics of M. cannonballus *ascospores*

The population dynamics of *M. cannonballus* ascospores from each location during the 3 year

period are shown in Figure 1. In July 1999, 2 months after muskmelon planting in fields A and B, initial ascospore density levels were higher in the fields which already had a muskmelon crop (1.49 and 1.32 ascospores g^{-1} of soil for fields A and B respectively) compared with fields C and D (0.62 and 0.45 ascospores g^{-1} of soil respectively), which were in fallow since autumn 1998.

In fields A and B, Monosporascus root rot/vine decline occurred in all cropping seasons. Perithecia of *M. cannonballus* were observed on affected roots and the fungus was isolated. In these fields the mean number of ascospores g^{-1} soil increased progressively, reaching a maximum 7 months after planting corresponding with 2–4 months after plant death. In field A, there were 2.34 and 2.25 ascospores g^{-1} of soil in November 1999 and December 2001, 2 and 3 months after plant death respectively. Similar results were obtained in field B, which had a maximum of 2.34 and 1.89 ascospores g^{-1} of soil in November 1999 and January 2001, 2 and 4 months after plant death respectively. These values represented, in general, an increase of ascospores compared with initial ascospore populations of more than 50%. In these fields, fallow periods resulted in a progressive decrease of ascospore levels in soil, reaching a value of 0.94 ascospores g^{-1} of soil in October 2000 for field A, between two muskmelon crops, and 0.88 ascospores g^{-1} of soil in April 2002 for field B after 2 years of fallow. Monthly data from soil samples collected in fields A and B during muskmelon cropping were used to compare in-bed and between-bed ascospore numbers (Figure 2). The results showed that, although in general the average number of ascospores g^{-1} of soil was higher in-bed than between-bed, there were no significant differences between them. The only exceptions were July 1999 in field B and August 2001 in field A.

In fields C and D, although there was some variability in ascospore numbers, a progressive decrease was observed during the study, decreasing from more than 1.0 ascospore g^{-1} of soil to 0.33 ascospores g^{-1} of soil in both fields in June 2002, at the end of the 3 year period.

Analysis of variance revealed that mean ascospore populations between fields A and B or C and

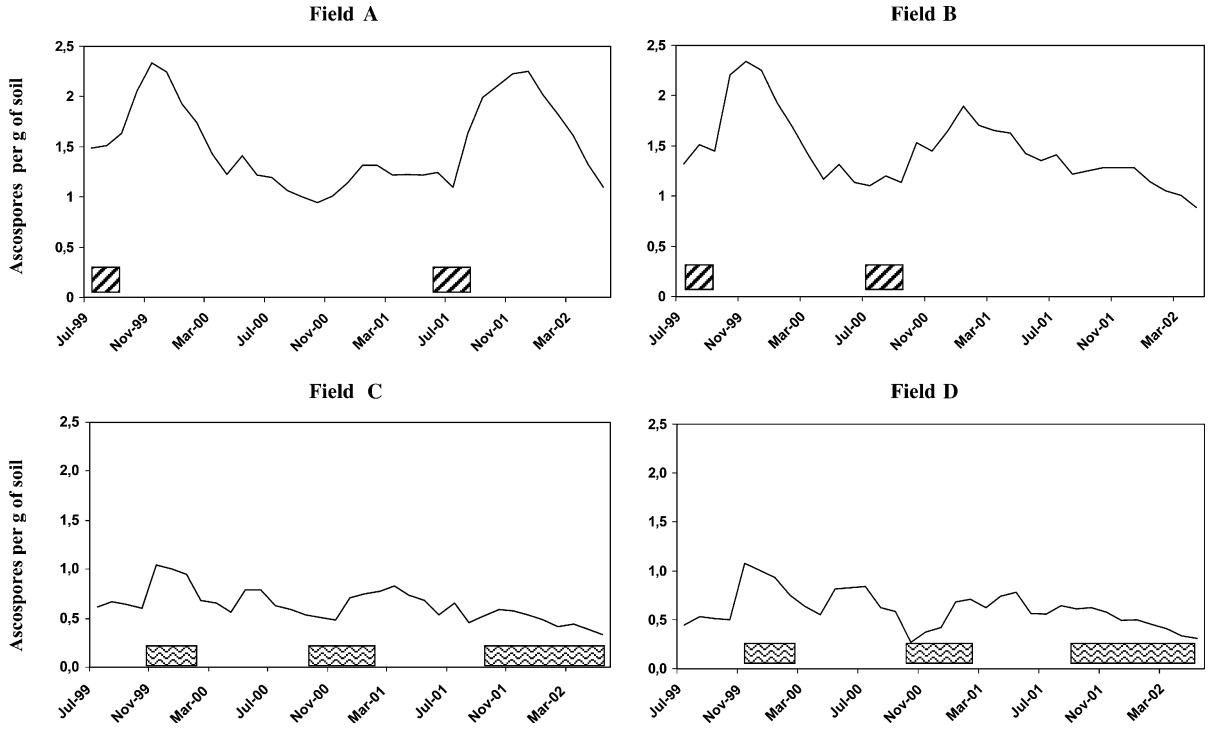

Figure 1. Dynamics of *Monosporascus cannonballus* ascospores (ascospores per gram of soil) in fields A, B, C and D during the 3-year period. (▨) Muskmelon crop; (▩) Flooding.

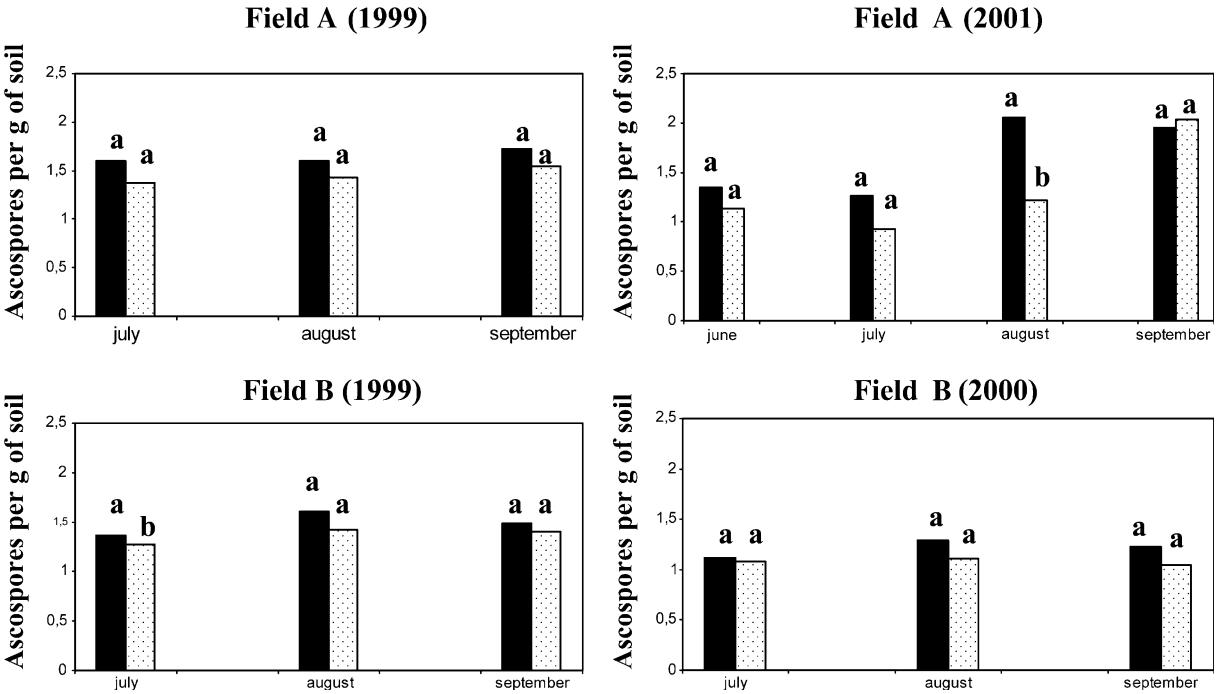

Figure 2. In-bed and between-bed comparisons of ascospore numbers (ascospores per gram of soil) in fields A and B, analysed by ANOVA using Tukey's multiple range test ($P = 0.05$). (■) In-bed; (▨) Between-bed.

D were not statistically different ($P = 0.337$ and $P = 0.590$ respectively). Therefore, data from these fields were combined for regression analysis.

For fields A + B, the relationship between ascospore mean population and months after muskmelon planting was studied (Table 2; Figure 3). The best fit ($P < 0.01$, $R^2 = 0.705$) corresponded to the equation $y = a + bx + cx^3$ in which a, b and c are parameters. The model showed the progressive increase of ascospores g^{-1} of soil after muskmelon planting, reaching the highest values 7 months after planting (2–4 months after plant death), and the later decline. For fields C + D the relationship between ascospore mean population and months after the beginning of soil sampling was studied (Table 2; Figure 4). The best fit ($P < 0.01$, $R^2 = 0.293$) corresponded to the equation $y = a + bx$. The model showed the progressive decrease of ascospores g^{-1} of soil in fields without muskmelon cropping during the period of study.

Isolation of M. cannonballus *from soil samples*

The isolation of *M. cannonballus* was achieved from muskmelon plants sown in all soil samples taken from March to June 2002 in fields A, B, and C. However, in field D, the fungus was isolated only from the soil samples taken in June 2002 (Table 3). The number of plants from which *M. cannonballus* was isolated was variable. The

Table 2. Regression analysis for the relationship between temporal variables (x) and ascospores per gram of soil (y) in fields A + B and C + D

Fields, regression model and independent variable	Regression data[a]				
	a	*b*	*c*	R^2	*P*-value
Fields A + B, ($y = a + bx + cx^3$) Months after muskmelon planting	0.73114	0.25770	−0.00156	0.705	0.0000
Fields C + D, ($y = a + bx$) Months after beginning of soil sampling	0.78644	−0.00941	–	0.293	0.0000

[a] *a*, *b*, *c*, regression coefficients; R^2, proportion of variation explained; *P-value*, ANOVA probability for the regression equation.

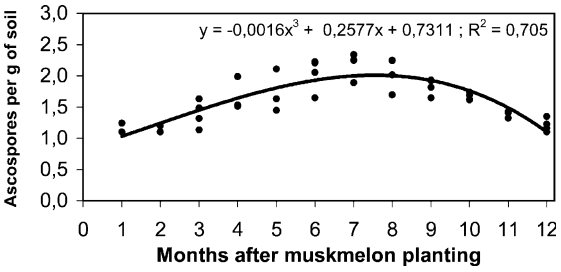

Figure 3. Relationship between months after muskmelon planting and ascospores per gram of soil in fields A + B.

isolation frequency varied from 1.2% in March and May for field C and May for field A, to 38.1% in June 2002 for field B. Regardless of fallow and flooding, ascospores of *M. cannonballus* were still present at the end of 3 years and were capable of causing infection.

Discussion

This work is the first to study the population dynamics of *M. cannonballus* ascospores in soil of muskmelon fields over a period of time. The Gleysols studied in this marsh area characteristically maintain a high water table during the spring-summer cropping season and can be flooded voluntarily for several months each year. Results obtained in fields A and B showed the progressive increase of the population of this soilborne ascomycete, which was maximum 7 months after muskmelon planting (2–4 months after plant death). Lobo-Ruano (1991) studied the biology of *M. cannonballus* on spring-summer muskmelon crops in Spain. This author indicated that perithecia can be detected on affected secondary or tertiary rootlets early in the growing season before vine decline symptoms could be observed. This could explain the progressive increase of the ascospore population, although highest values appeared after plant death. In Israel, Pivonia et al. (2002) demonstrated that 50% of the examined muskmelon root segments were colonized by *M. cannonballus* 42 and 67 days after planting in autumn and winter crops respectively, and mature perithecia were observed on dead secondary and tertiary roots before fruit maturation. In Arizona and California the induction of the sporulation of *M. cannonballus* under field conditions appears to coincide with root death and, as a consequence, significant pathogen reproduction occurs primarily after the crop has been terminated (Stanghellini et al., 2004a). Waugh et al. (2003) studied the reproductive potential of *M. cannonballus* and indicated that the root system of a single mature cantaloupe plant infected by this pathogen is capable of supporting the production of approximately 400,000 ascospores. The latter population, if incorporated uniformly into soil, would be equivalent to 10 ascospores per gram of soil. As a consequence, the delay of the maximum ascospore population in relation to plant death (2–4 months) could be the result of the progressive decomposition of root systems of the plants. In this sense, Waugh et al. (2003) and Stanghellini et al. (2004b), indicated that the removal of infected roots at the end of the crop would be a method of preventing inoculum build-up in soil, although they also commented that practices employed by some growers at crop termination, such as foliar application of herbicides or the mechanical destruction of vines, could be counterproductive with respect to disease management because they enhance rather than inhibit reproduction of *M. cannonballus*.

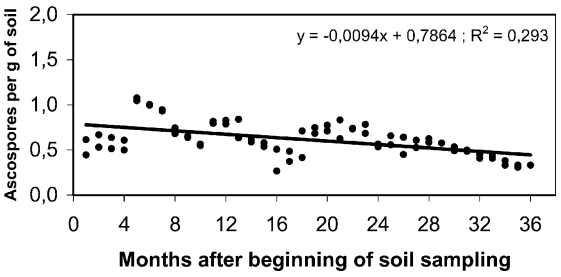

Figure 4. Relationship between months after beginning of soil sampling and ascospores per gram of soil in fields C + D.

In fields A and B, when we compared in-bed and between-bed ascospore numbers during muskmelon cropping, in general, there were no statistical differences. Mertely et al. (1993b) obtained a similar result when they quantified the number of ascospores of *M. cannonballus* in the soil of one intensively managed muskmelon field in South Texas, probably because root densities at 10–20 cm depth are uniform for in-bed and between-bed samples.

Monosporascus root rot/vine decline is a monocyclic disease since *M. cannonballus* has no known anamorph stage and only forms ascospores

Table 3. Number of plants colonized by *Monosporascus cannonballus* and isolation frequency in bioassays conducted with soil samples taken from March to June 2002 in fields A, B, C and D

Field	March		April		May		June	
	No of plants[a]	Isolation freq (%)[b]	No of plants	Isolation freq (%)	No of plants	Isolation freq (%)	No of plants	Isolation freq (%)
A	2	3.6	6	17.9	1	1.2	5	22.6
B	2	2.4	3	6.0	3	10.7	5	38.1
C	1	1.2	2	7.1	1	1.2	5	14.3
D	0	–	0	–	0	–	2	4.8

[a]Number of plants from which *M. cannonballus* was isolated (isolations were made from six plants).
[b]Percentage of 84 root fragments from which *M. cannonballus* was isolated.

near the end of the season (Martyn and Miller, 1996; Waugh et al., 2003); thus initial inoculum density in soil could be relevant for anticipating the expected disease level. Waugh et al. (2003), commented that known problem fields contain as few as 2 ascospores g^{-1} of soil. The population dynamics of ascospores of *M. cannonballus* found in fields A and B showed that the ascospore levels 12 months after muskmelon planting were similar to the initial ascospore counts, between 1 and 1.5 ascospores g^{-1} of soil. This was confirmed by regression analysis with an increase of ascospore density to a maximum, followed by a decrease to a background level over time. This dynamic suggests antagonistic interactions between pathogens and other microorganisms or the soil fauna (Gilligan, 1994). A rapid increase of inoculum density could be associated with more intensive management practices, as pointed out by Mertely et al. (1993b), who found a mean of 11.1 ascospores g^{-1} of soil in an intensively managed field in Texas.

In fields C and D, which were in fallow and had extensive flooding periods, there was a progressive decrease in the mean population of ascospores of *M. cannonballus*, which was of 0.33 ascospores g^{-1} of soil for both fields at the end of the 3 year period.

In this work, we used the isolation of *M. cannonballus* from muskmelon seedlings grown in soil samples to verify that the ascospores, which function as the primary inoculum for root infection (Stanghellini et al., 1996, 2000), were viable and capable of infecting at the end of the study. Martyn and Miller (1996) indicated that ascospores of *M. cannonballus* were presumably long-lived and could serve as a long-term survival structures. Although ascospores can be extracted from soil, it is difficult to determine their viability because they do not germinate or germinate very rarely under laboratory conditions (Mertely et al., 1993b). Stanghellini et al. (1996, 2000) assessed the germination of naturally as well as culturally produced ascospores in soil and demonstrated the role of soil actinomycetes in this process, but they indicated that it is difficult to quantitatively determine the viability of the resident ascospore soil populations.

We obtained successful root colonization by *M. cannonballus* in the bioassays conducted with all soil samples taken from March through to June 2002 for fields A, B and C and only from the soil samples taken in June 2002 for field D. More importantly, ascospores survived in fields C and D, in which no muskmelons were grown during three years, and fields were flooded for a total of 21 months. This demonstrates that the ascospores of *M. cannonballus* can survive for at least 3 years in the absence of adequate hosts and also that this fungus seems to be well adapted to survive in soils which maintain a high water table during the crop, or under flooding conditions.

We do not know if weeds could have been involved in perpetuation of *M. cannonballus* in these fields. There is some evidence that this fungus can infect and reproduce on some non-cucurbit hosts (Mertely et al., 1993a; Martyn and Miller, 1996), although perithecia or ascospores of *Monosporascus* spp. have never been observed from roots of weeds grown in the area of study. Isolations from representative weed species (*Amaranthus blitoides*, *A. hybridus*, *A. viridis*, *Chenopodium album*, *C. murale* and *Portulaca oleracea*) were unsuccessful (unpublished data).

In this study, the survival of ascospores of *M. cannonballus* for a 3 year period of time has been assessed but, at the same time, we have observed the decrease in ascospore populations in

fields A and B between muskmelon cropping, and in fields C and D, which were in fallow and flooded for several months. The role of fallowing or flooding fields as cultural methods for the management of the soilborne pathogens has been emphasized by several authors (Katan, 2000). Bell and Sumner (1987) demonstrated that a 40 week fallow period would be effective in reducing populations of *Rhizoctonia solani* and other pathogenic soilborne basidiomycetes. Verticillium wilt of cotton, caused by *Verticillium dahliae*, was effectively controlled by long-term summer soil flooding with or without paddy rice culture in California (Pullman and DeVay, 1981). Cintas and Webster (2001) recommended winter flooding as the best alternative to rice straw burning for reducing inoculum of *Sclerotium oryzae*, causal agent of rice stem rot. However, according to our results, fallowing or flooding muskmelon fields seem to be only marginally effective for managing soilborne inoculum of *M. cannonballus*.

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