Seed bank and established vegetation in the last remnants of the Mexican Central Plateau wetlands: the Lerma marshes

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Received 03-III-2013. Corrected 20-X-2013. Accepted 20-XI-2013.

Abstract: Banco de semillas y vegetación establecida en los últimos remanentes de los humedales de la Meseta Central Mexicana: las ciénagas de Lerma. Seed banks play a central role in vegetation dynamics of many wetlands. Therefore, knowledge of seed reservoirs in the soils of aquatic communities should provide useful tools for conservation and restoration efforts. This study was conducted in the Lerma marshes, one of the last remnants of the vast wetlands that were once in the Mexican Central Plateau. The main objective was to determine the composition and abundance of seed bank and its relationship with established vegetation of the three Lerma marshes. In each marsh, we systematically selected 18 to 40 sampling sites. In each site, the composition of vascular plant vegetation was evaluated in two 10m lines perpendicular to the shore. Every 0.5m, we determined the coverage of species by measuring the intercepted length for each plant or group of plants. At each sampling site where we had evaluated the established vegetation, we collected a sample of the top 10cm of sediment; the soil cores were divided into an upper layer (0-5cm) and a lower layer (5-10cm). These samples were used to evaluate the seed bank by the seedling emergence method. All samples were placed in a greenhouse at 20-25ºC and remained flooded for 15 weeks. Forty-nine species were recorded in the vegetation. Chiconahuapan had the richest and most diverse flora and the greatest number of perennial species. A life-forms analysis showed that perennial herbs, especially rooted-emergent hydrophytes, dominated in the three wetlands. Sixty-one species were identified in the total seed bank; Chimaliapan had the most diverse total seed bank, whereas the mean seedling density was higher in Chignahuapan. Only two species of the total seed bank of each marsh had a density greater than 10% of the total, and more than half were uncommon. The upper layer of sediment (0-5cm) contained two times more seeds/m^2 and species per sample than the lower layer (5-10cm), and there was a significant decrease of seed density with depth. The detrended correspondence analysis produced a clear separation between the composition of the seed banks and established vegetation. In general, in each marsh there was less species diversity in the established vegetation than in the seed bank. Dominance by a few species in the seed bank, the presence of opportunistic species, and the low representation of established species in the seed bank suggest wetland degradation and a low probability of regenerating the natural communities from the seed bank. To ensure the permanence of these marshes, their biodiversity, and therefore the environmental services they provide, up to date planning is a must, and efforts to control and monitor hydrology, water quality, and the influence of human activities are suggested. Rev. Biol. Trop. 62 (2): 455-472. Epub 2014 June 01.

Key words: Chignahuapan, wetlands diversity, flora, hydrophytes, Mexico, degraded wetlands, wetland restoration, upper Lerma River basin.

Seeds stored in the soil are a source of diversity accumulated under different environmental conditions over time, so they constitute a historical basis and the potential future of the vegetation (Hopfensperger, 2007; Fhiser, Loneragan, Dixon, & Veneklaas, 2009). The seed bank has an important role in the composition, establishment, and persistence of plant communities in aquatic environments, especially after a disturbance because it allows a rapid response by the vegetation (Leck, 1989; Galatowitsch & van der Valk, 1996). The number of species in the seed bank reflects the diversity of the community, but in different aquatic systems, the composition of the seed bank is temporal and spatially variable, as is its relationship with the established vegetation (Leck, 1989; Cronk & Fennessy, 2001). In most wetlands, the composition of the seed bank is strongly related to the established plant community (Leck & Simpson, 1987; Ungar & Woodell, 1996b; Lui, et al., 2006), though in some aquatic environments, there is low similarity, both in the richness and the relative abundance of the species (Smith & Kadlec, 1983; Leck & Simpson, 1987; Wilson, Moore, & Keddy, 1993; Egan & Ungar, 2000; Gordon, 2000; Combroux, Bornette, Willby, & Amoros, 2001; Lui, Zhou, Li, & Cheng, 2005; Etchepare & Boccanelli, 2007; Xiao, Dou, & Lui, 2010).

The composition of the seed bank provides an idea of which species are vulnerable to local extinction and which potentially can colonize a site if the hydrology is altered (Cronk & Fennessy, 2001). Therefore, analysis of the seed bank and of the established vegetation may indicate the successional stage of the community (van der Valk & Davis, 1978). If we know the diversity of the seed bank, its relationship to standing vegetation, and its responses to different environmental factors, we have a useful tool for conservation and restoration of aquatic systems (Middleton, 1999; Chang, Jefferies, & Carleton, 2001; Hugh & Kimberley, 2007; Nishihiro, Nishihiro, & Washitani, 2006; Valkó, Török, Tothmérész, & Matus, 2011; Ge, Liu, & Wang, 2013).

We investigated differences in the vegetation and seed bank of three Lerma marshes, an important region in Mexico that preserves the last remnants of the formerly vast wetlands of the Mexican Central Plateau. The high diversity of the Lerma marshes allowed its protection since 2002 by the National Commission of Natural Protected Areas. Mexican law treats these marshes as natural protected areas (Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT], 2002; Perez & Valdez, 2006), bird conservation areas, and a priority habitat for more than 20 resident and migratory waterfowl (Ramsar Convention on Wetlands, 2006). At present, because there is no management plan focused on local uses, these areas are gradually being reduced in size due to natural hydrological changes and, principally, by human actions (Zepeda, Antonio, Lot, & Madrigal, 2012a). The current balance indicates a great fragility of these systems that have different degrees of disturbance, pollution, desiccation, and fragmentation, which all have a negative impact on biodiversity (Ramsar Convention on Wetlands, 2006).

Studies on aquatic vegetation, especially the aquatic seed bank, are required to understand the wealth and size of the seed reserve in the soil and to characterize its vegetation restoration potential in these degraded environments. This study addressed three questions: First, does the species richness and density of the vegetation and seed bank differ among the marshes? Second, are there significant differences in the species composition and the density of the seed bank with sediment depth? Third, what is the relationship between the seed bank and the composition of the established vegetation in each marsh?

MATERIALS AND METHODS

Study site: The study area comprises three Lerma marshes located in the highest elevation area of the Upper Lerma River Basin in Central Mexico. They are the remains of extensive wetlands that formed a continuum of 27 000ha at the end of the 19th century in the state of Mexico (Martinez, 1993). Currently, its size is much smaller and only covers about 3 000ha, which is fragmented into three major and permanent water bodies. The Chignahuapan (Cg) marsh (19º08’49” N - 99º31’11” W) that covers about 600ha and is located at an altitude of 2 580m. The Chimaliapan (Cm), which is the largest of the three marshes, with an area of about 2 100ha (19º14’28” N - 99º20’50” W), and located at 2560m above sea level. And the marsh of Chiconahuapan (Cc), that covers about 350ha (19º21’19” N - 99º30’17” W), located in the same elevation (Fig. 1).

Climate is temperate subhumid with summer rains and an average annual temperature of 12°C. Average annual precipitation is 800 to 1200mm, with 80% occurring from May to September (Vásquez, 1999). The fields surrounding the marshes have an intense agricultural land use. The Lerma marshes are herbaceous wetlands in which there is a clear zonation of vegetation related to the flood level. There are wide peripheral bands of marshes subject to seasonal flooding where the maximum depth does not exceed 1.5m and the vegetation is mainly a community of rooted emergent hydrophytes, known locally as “tulares” (Ramos, 2000). The amount of land flooded in each lake is affected by rainfall; in some areas, six to eight months of prolonged flooding alternates with dry land the rest of the year. Less than 35% of the current area of each marsh has open and permanent

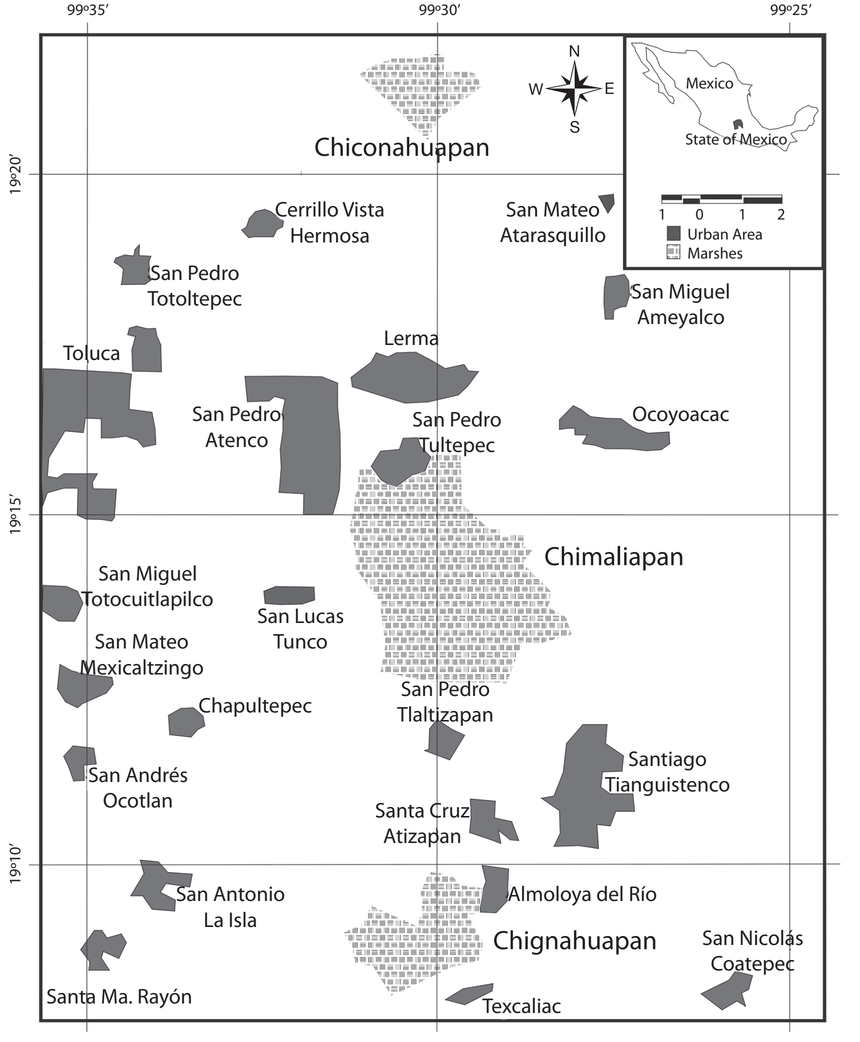

Fig. 1. Location of the Lerma marshes.

waters with a maximum depth of 2.5m; in these areas, submerged and free-floating hydrophytes are common.

Sampling of vegetation and seed bank: To describe and characterize the dominant vegetation of the marshes and the species diversity of the seed bank, in September 2008 (rainy season), we systematically selected 18 to 40 marsh sampling sites based on the wetland area and accessibility (maximum water level of 1m). Within each marsh, the distance between sites was at least 50m to cover as wide an area as possible.

In each site, the composition of vascular plant vegetation was evaluated; we placed two 10m lines perpendicular to the shore. Every 0.5m, we determined the coverage of species by measuring the intercepted length for each plant or group of plants; this information is described in Zepeda, Lot, Antonio, & Madrigal (2012b).

At each sampling site where we had evaluated the established vegetation, we collected a sample of the top 10cm of sediment and separated it into an upper layer (0-5cm) and a lower layer (5-10cm) sample in the field (Lui et al., 2005). Eighteen sediment samples were collected in the littoral zone of Cg, 19 in Cc, and 40 in Cm. For this purpose, we used a cylinder of 4.5cm in diameter and 60cm in length (0.00159m^2 surface area); samples were included in airtight bags and stored in a 3°C dark room for a month. The cumulative sampling area for each marsh was 0.0286m^2 for Cg, 0.0302m^2 for Cc, and 0.0636m^2 for Cm.

Seed bank samples were collected after the main season for field germination and before massive seed dispersal in 2008. The seed bank was evaluated by the seedling emergence method according to van der Valk & Davis (1978). Samples from each sampling site and each depth were placed separately in 15cm diameter pots on top of a 1cm layer of sterilized coarse sand. Five pots containing only sterilized sands were placed among the sample pots to test for contamination by local seeds; no seedlings were found in these control pots during the course of the germination test. We carefully removed tubers, rhizomes, and visible roots from the samples before spreading them out. The pots were randomly distributed in a greenhouse at 20-25ºC with natural light conditions, and remained flooded (with a maximum water level of 1cm above the ground) for 15 weeks. The pots were reviewed every three days to observe the germination and growth of seedlings. All emerged seedlings were identified and counted to assess the density and richness of the seed bank of each study area and the sediment depth. Once the seedlings were counted and identified, they were removed to avoid competition.

For the established vegetation, the species richness was determined as the total number of species along all transects of each site (Magurran species richness; Magurran, 2004). The relative cover of each species was calculated as the sum of transect lengths intercepted divided by the sum of total transect lengths intercepted by all species. These values were grouped into five categories: I<1%, II=1-5%, III=5.1-10%, IV=10.1-20%, and V>20%. The frequency of each species was calculated as the percentage of places where the species was present in relation to the total evaluated places in each marsh. The frequency of each species in each marsh was compared by using the Chi-square test.

In the seed bank, the species richness was also determined using Magurran species richness (Magurran, 2004). The density of germinated seeds was determined as the number of seedlings per sample per square meter (Begon, Townsend, & Harper, 2006). The total density of the seed bank of each marsh was estimated by combining the density values obtained in the two sediment depths and they were compared using a one-way analysis of variance. The number of species per sample and seedlings/m^2 for the two sediment depths (0-5 and 5-10cm) and for each marsh were compared using a nested ANOVA, with the depth nested within the marshes. The frequency of seedlings from the seed bank was estimated as the percentage of all samples where the species was present in each marsh; these were compared by a Chi-square test.

We calculated the Shannon-Wiener index (Brower, Zar, & Ende, 1997; Begon et al., 2006) to determine the diversity of the total seed bank for each marsh; diversity values for vegetation were obtained from Zepeda et al. (2012b). These analyses were made using the Past 1.90 program (Hammer, Harper, & Ryan, 2001). We compared diversity indices from seed bank and vegetation considering all pairwise comparisons among the three marshes using a modified Student's t-test (Zar, 2010).

The floristic similarity between the vegetation and the total seed bank of each marsh was calculated by using the Sorensen coefficient (Moreno, 2001). The relationship between the established vegetation and the total seed bank from the three marshes was determined using detrended correspondence analysis (DCA) in the Past 1.90 program (Hammer et al., 2001). To establish the relationship of species abundance to the seed bank and vegetation, we used a Spearman's rank correlation. The percentages of the life forms recorded in the seed bank and vegetation of each wetland were compared with a Mann-Whitney test. Categories of life forms were established according to Sculthorpe (1985). The univariate analysis and nested ANOVA were made in the Statistica 7 program (StatSoft Inc., 2003).

RESULTS

Vegetation: A total of 49 different species were recorded in the established vegetation of the three marshes, with 20 species in Cg, 27 in Cm, and 29 in Cc. Species richness was statistically similar among the wetlands (Table 1), but the floristic similarity, diversity, and coverage showed differences among the three marshes.

The three wetlands shared seven species. 17 were common between Cm and Cc, which is a floristic similarity of 61% (Table 2). The floristic similarity between Cg and the other two marshes was less than 50% (Table 2). The Cc vegetation was more diverse than the vegetation of the other two marshes (Fig. 2). There were 20 species that had coverage greater than 1% in Cc and 12 in Cg and Cm (Table 1). The remainder can be considered as rare species because their coverage was 1% or less. In Cg, those species with high coverage (10% to >20%) were *Eleocharis macrostachya* Britton, *Poa annua* L., *Schoenoplectus californicus* (C. A. Meyer) Soják, and *Ranunculus cymbalaria* Pursh, whereas in Cm, they were *Hydrocotyle ranunculoides* L., *Jaegeria bellidiflora* (Sessé and Moc. ex DC.) Torres and Beaman, *Paspalum distichum* L., and *Sagittaria macrophylla* Zucc. In Cc, only *Myriophyllum heterophyllum* Michx. and *S. californicus* had a high coverage (Table 1). In Cg and Cm, three species had a frequency >10%, and in Cc there were six. The frequency of seven species varied significantly in the vegetation of the three marshes ($p<0.05$, Chi square). *Eleocharis macrostachya*, *Polygonum hydropiperoides* Michx, and *Poa annua* were significantly more frequent in Cg than in the other two marshes, whereas *Eleocharis densa* Benth. and *Ludwigia peploides* (Kunth) P. H. Raven were significantly more frequent in Cc than in Cm and Cg. Only *S. macrophylla* was statistically more frequent in Cm than in Cc (Table 1).

Seed bank: More species occurred in the seed bank than in the established vegetation. A total of 61 species were identified in the seed bank, with 27 in Cg, 46 in Cm, and 34 in Cc. There were 13 that were common to all three wetlands (Table 1), and 23 were shared between Cm and Cc, and between Cm and Cg. The three marshes were significantly different in seed bank floristic composition, species diversity, mean seedling density, species frequency, and between the two sediment depths.

The Cm total seed bank was more similar to the Cg bank (63%) than to the Cc bank (57%), while the lowest similarity was found between Cg and Cc (42%, Table 2). The species diversity was significantly greater in Cm (Fig. 2). The mean number of species per sample from the total seed bank did not differ statistically among the three marshes ($F=2.1$, $p=0.1$, Fig. 3). The mean seedling density of

TABLE 1

Recorded parameters of vegetation and seed bank species in the Lerma marshes. Relative density, relative frequency and coverage found for standing vegetation. For seed bank, relative frequency and germination density by sediment depth (0-5, 5-10cm)

	Vegetation									Seed bank											
	Relative density (%)			Relative frequency (%)			Coverage*			Density seedlings/m^2									Total frequency (%)		
										Depth (0-5 cm)			Depth (5-10 cm)			Total (0-10 cm)					
	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc
Richness	22a	27a	29a							23a	40b	29ab	19a	30a	25a	27a	46b	34ab			
Density plants/m^2										86 889	81 673	79 745	33 102	42 669	62 227	76 947	90 626	10 1114	3	3	3
Agrostis perennans		1.4			1.5			II						629			629			0.03	
Arenaria bourgaei	0.3			0.3			I			5 659	629		629	629		2 305	943		0.17a	0.05b	
Arenaria paludicola	0.7			1.5			I			3 458	1 886		629			2 892	629		0.28a	0.03b	
Aster subulatus	0.9	0.8		2.3	1.6		I	I			629		629	838		629	943		0.06a	0.20b	
Berula erecta		4.0	1.3		6.0	2.2		II	II						1 258			1 258			0.05
Bidens aurea			0.5			2.2			I												
Bromus dolichocarpus										2 829						2 829			0.11		
Callitriche deflexa										4 401	629	1 527	629	3 982	2 515	2 515	4 925	2 605	0.11a	0.6b	0.36c
Ceratophyllum demersum			0.3			0.6			I												
Cyperus niger											943						2 358			0.10	
Cyperus semiochraceus			1.4			2.8			II												
Cyperus sp.												2 201		629	943		629	2 096		0.03a	0.16b
Echinochloa holciformis	6.0	5.4		6.0	6.0		III	III			2 358		1 886	629	2 515	1 886	838	2 515	0.06a	0.15b	0.05c
Echinochloa oplismenoides											629						1 258			0.03	
Eichhornia crassipes		2.7			3.8			II													
Eleocharis acicularis										8 226	1 572	1 258	4 042	6 209	6 288	4 318	10 596	3 773	0.83a	0.67 b	0.21 c
Eleocharis bonariensis		1.2	0.8		0.6	1.1		II	I												
Eleocharis densa	0.6	6.8	3.4	0.8a	5.4ab	7.2b	I	III	II												
Eleocharis dombeyana										4 087	943	7 126	3 694	4 323	10 060	5 397	4 454	7 860	0.67a	0.30 b	0.21c
Eleocharis macrostachya	16.0	8.3	1.1	13a	5.5ab	1.7 b	IV	III	II												
Eleocharis montana		1.3			0.6			II			755	3 144	1 572	1 467		1 572	1 808	3 144	0.11ab	0.20a	0.05b
Epilobium ciliatum	1.0		1.5	2.3		3.4	II		II	629	8 724	2 767			838	629	1 572	2 725	0.11a	0.05b	0.31c
Euphrosyne partheniifolia										4 821	3 458	629	3 694	2 874	629	5 030	2 585	629	0.78	0.45	0.21
Galinsoga parviflora												2 201						2 201			0.11
Glyceria fluitans											12 575			1 258	1 886		13 833	1 886		0.03	0.05

TABLE 1 (Continued)

	Vegetation									Seed bank											
	Relative density (%)			Relative frequency (%)			Coverage*			Density seedlings/m^2									Total frequency (%)		
										Depth (0-5 cm)			Depth (5-10 cm)			Total (0-10 cm)					
	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc
Glyceria mexicana											3 773			1 258			2 934			0.08	
Gnaphalium americanum											3 301	629			629		2 305	629		0.15	0.16
Gnaphalium luteo-album										5 030	1 069	2 410		1 415	2 096	5 030	1 768	3 458	0.06a	0.40b	0.32c
Hydrocotyle ranunculoides	7.8	11.7	7.5	7.8	11.8	13.4	III	IV	III		629			786			1 006			0.25	
Hydrocotyle verticillata	6.0			5.0			III			5 030						5 030			0.06		
Hydromystria laevigata		0.3	6.1		0.5	9.5		I	III												
Jaegeria bellidiflora	3.6	16.1	4.2	5.5	13.5	8.9	II	IV	II	6 29	629					629	3 458		0.06	0.05	
Jaegeria glabra			0.2			1.1			I			3 144						3 144			0.05
Juncus aemulans											629	2 829			629		1 886	3 144		0.03a	0.11b
Juncus arcticus											2 044	17 291			629		1 886	16 453		0.03a	0.32b
Juncus effusus		1.1	0.8		0.5	1.1		II	I						2 515			2 515			0.05
Juncus tenuis												5 973			10 563			10 959			0.37
Leersia hexandra		3.9			3.0			II													
Lilaea scilloides	0.0	0.6		0.3	0.9		I	I			1 006						1 886			0.03	
Lilaeopsis schaffneriana	8.7	2.1	3.3	6.8	2.8	6.1	III	II	II	12 306	2 485	2 012	1 153	1 886	4 087	8 460	3 598	3 301	0.61	0.45	0.42
Limosella aquatica										1 886	1 886	1 572	1 572	1 429	943	1 729	1 761	2 515	0.44a	0.37b	0.11c
Ludwigia peploides		1.0	5.1		0.8a	12.8b		I	II					1 258	629		1 258	629		0.05	0.11
Marsilea mollis			0.4			0.6			I												
Mecardonia procumbens												943						943			0.11
Mimulus glabratus	0.1			0.3			I				2 305						629			0.05	
Myriophyllum aquaticum		3.3	4.3		3.0	7.8		II	II												
Myriophyllum heterophyllum			20.7			31.8			V			629			629			838			0.16
Najas guadalupensis												629		629	629		629	629		0.03a	0.11b
Nierembergia angustifolia												1 258						1 258			0.05
Nymphaea gracilis		0.2			0.1			I													
Nymphoides fallax			3.1			9.5			II			1 258			943			1 048			0.16
Oxalis corniculata.											2 021						629			0.03	
Paspalum distichum		10.3	5.0		5.8	17.9		IV	II												
Poa annua	15.0			11.8			IV														

TABLE 1 (Continued)

	Vegetation									Seed bank											
	Relative density (%)			Relative frequency (%)			Coverage*			Density seedlings/m^2									Total frequency (%)		
										Depth (0-5 cm)			Depth (5-10 cm)			Total (0-10 cm)					
	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc	Cg	Cm	Cc
Poaceae 1										943			629			838			0.17		
Poaceae 2												629						629			0.16
Polygonum hydropiperoides	3.5	0.1	2.0	0.3	0.4b	5.0c	II	I	II												
Polygonum lapathifolium	0.5	1.8		0.8	2.6		I	II		1 132	943		1 132	1 886		1 258	2 829		0.50	0.30	
Polygonum mexicanum		0.3			0.8			I		629	2 695			629		629	1 006		0.06a	0.25b	
Polygonum punctatum	1.9	4.4	1.3	4.8	5.0	5.6	II	II	II	943	1 258	838	629			786	943	838	0.22a	0.05a	0.16c
Potamogeton illinoensis			4.1			6.1			II												
Potamogeton nodosus		0.4	1.6		0.4a	5.0b		I	II												
Ranunculus cimbalaria	12.4			9.8			IV			9 117			1 572			7 231			0.44		
Ranunculus dichotomus											1 006			629			838			0.08	
Ranunculus trichophyllus												629			1 572			1 258			0.16
Rorippa mexicana										629	2 378	1 707		629	943	629	629	1 965	0.11 a	0.05 b	0.42 c
Rorippa pinnata	0.5			2.3			I			10 731	3 563	3 301	5 659	796	2 515	10 514	2 298	5 156	0.04	0.72 b	0.26 c
Rumex crispus	0.2			0.5			I														
Rumex flexicaulis										629	1 886		1 048	629		880	1 048		0.28 a	0.08 b	
Rumex obtusifolius														629			629			0.05	
Sagittaria macrophylla		10.3	0.1		17.1 a	0.6b		IV	I												
Schoenoplectus californicus	14.3		14.7	13.0		17.9	IV		IV												
Schoenoplectus tabernaemontani		0.4	0.6		0.3	1.7		I	I	2 515	1 572		1 048	2 201		1415	1 617		0.22	0.18	
Sisyrinchium convolutum														629			629			0.03	
Soliva anthemifolia											629		1 258			1258	629		0.06	0.03	
Tillaea saginoides											1 258	1 572					629	1 572		0.05	0.11
Trifolium sp.											629						629			0.03	
Tripogandra purpurascens											2 892						629			0.05	
Typha latifolia			4.1			25.7			III		1 886	7 755		629	5 345		629	5 659		0.13 a	0.26 c
Urtica dioica	0.1		0.5	0.3		2.8	I		I		943	1 886		629			755	1 886		0.13	0.05
Veronica peregrina ssp. *xalapensis*										629	629			629		629	629		0.06	0.05	

Cg=Chignahuapan, Cm=Chimaliapan, Cc=Chiconahuapa. *The vegetation cover categories are I<1%, II=1% to 5%, III=5.1%-10%, IV=10.1%-20%, and V>20%. Different letters indicate significant differences between the relative frequency of the established vegetation and seed bank, and richness of each Lerma marsh, using a Chi-square test with a significance of $p<0.05$.

TABLE 2
Sorensen similarity coefficient (%) between the vegetation and total seed bank of the Lerma marshes

	Vegetation			Seed Bank	
	Cg	Cm	Cc	Cg	Cm
Vegetation					
Cm	48				
Cc	39	61			
Seed Bank					
Cg	48	32	17		
Cm	36	35	24	63	
Cc	25	23	34	42	57

Cg=Chignahuapan, Cm=Chimaliapan, Cc=Chiconahuapa. Total seed bank was calculated adding the values from sediment depths (0-5, 5-10 cm).

the total seed bank was about 60% higher in Cg (F=4.1, p=0.01, Fig. 3) than in the other two marshes. Cm and Cc showed no significant differences in the density of germinated seeds (p>0.05, least significant differences [LSD], Fig. 3). Over 90% of the species in each marsh had a density equal to or less than 10% of all the recorded seedlings, and in each marsh, only two species had a density >10% of the total. In Cg, *Rorippa pinnata* (Moc. and Sessé) Rollins (10 500seedlings/m^2) and *Lilaeopsis schaffneriana* (Schltdl.) Coult. and Rose (8 500seedlings/m^2) were the species with the highest number of seedlings per square meter. In Cm, these were *Glyceria fluitans* (L.) R.Br. (13 800seedlings/m^2) and *Eleocharis acicularis* (L.) Roem. et Schilt. (10 600seedlings/m^2), and in Cc, these were *Juncus arcticus* Willd. (16 500seedlings/m^2) and *Juncus tenuis* Willd. (11 000seedlings/m^2).

The Chi-square test showed that the frequency of 21 species varied significantly among marshes (Table 1), with nine species significantly more frequent in Cg than in the other two marshes. In Cc and Cg, 12 species had a frequency >20% with just 11 in Cm. The species with a frequency >20% and common to all three wetlands were: *L. schaffneriana*, *Eleocharis dombeyana* Kunth, *Euphrosyne partheniifolia* DC., *E. acicularis* and *R. pinnata* (Table 1). More than half of the species found in the wetlands were rare (defined as a frequency of 20% or less in the seed bank). Cm was the marsh with significantly more rare species (76%) than Cg (55%) and Cc (64%).

Of the 39 rare species in the seed bank, 12 were unique to Cm, 10 to Cc, and 3 to Cg. Only two rare species in the seed bank were common to all three wetlands, five were common between Cm and Cg, with eight species common between Cm and Cc (Table 1).

The upper sediment layer (0-5cm) had more species than the lower layer (5-10cm). These differences were significant for each marsh (Table 3, Fig. 3). The species number per sample for each depth did not differ among the marshes (Table 3, Fig. 3). The aquatic and subaquatic plants found in the Cg upper sediment layer were *J. bellidiflora*, *Epilobium ciliatum*

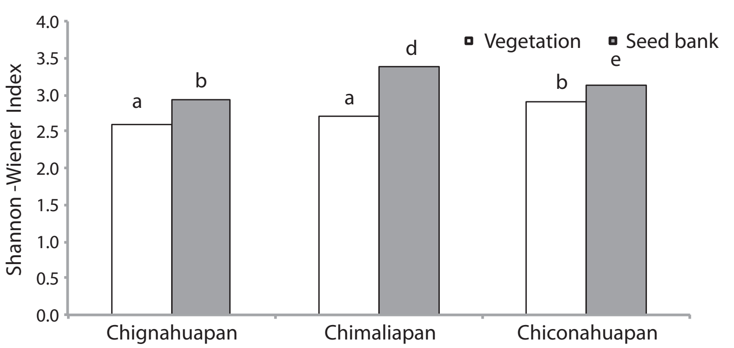

Fig. 2. Shannon-Wiener diversity for the established vegetation and the total seed bank for the Lerma marshes. Different letters represent the significant differences between pairwise of samples, using a modified Student's *t*-test (Zar, 1999) with a significance of 0.05.

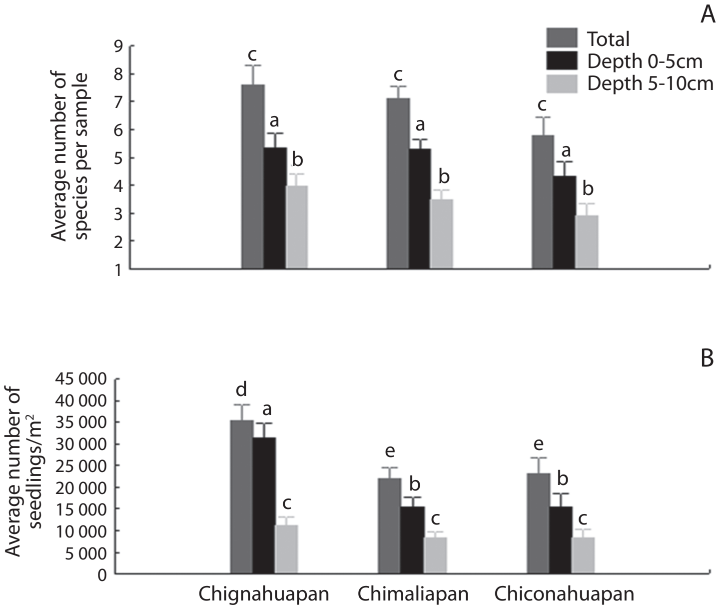

Fig. 3. Mean species per sample **(A)** and mean seedling density **(B)** of the seed bank of the Lerma marshes at two depths (0-5, 5-10cm) and total (combining the values of the sediment depths). Values are mean±standard error. In the total seed bank we used a one-way ANOVA ($p<0.0001$). The differences between depths within and among the marshes were compared with a nested ANOVA, F values shown in Table 3. The error bar followed by different letters indicates significant differences among variables ($p<0.001$).

TABLE 3
Values of nested ANOVA for the mean number of species per sample and mean seedlings/m^2 among marshes and sediment depths (0-5, 5-10cm)

	Mean species per sample			Mean seedlings per m^2		
	df	*F*	p	df	*F*	p
Marshes	2	2.5	0.0830	2	9.1	0.0001*
Depths	1	17.5	0.000048*	2	33.1	0.000001*
Residual	148			148		

The main effect is the swamps and sediment depths are nested into the marshes. *Significant differences.

Raf., and *Hydrocotyle verticillata* Thunb. In Cm, there were the first two and *Echinochloa oplismenoides* (Kunth) Chase, *Cyperus niger* Ruiz and Pavón, *Lilaea scilloides* (Poir.) Hauman, and *Mimulus glabratus* Kunth. In Cc, we only found *Mecardonia procumbens* (Mill.) Small, *Nierembergia angustifolia* Kunth, and *Jaegeria glabra* (S. Watson) B.L. Rob. in the upper sediment layer.

In the three marshes, the mean seedling density decreased significantly with depth (Table 3, Fig. 3). In Cg, 72% of all emerged seedlings grew from the upper sediment layer, with 65% in Cm and 56% in Cc. Only the upper sediment layer varied significantly among the wetlands. In this sediment depth, Cg had more than double the number of seedlings per square meter (31 000seedlings/m^2) compared with the other two marshes (Table 1, Fig. 3).

Several species were present at both depths, but some were more abundant in the upper sediment layer, e.g., in Cg, they were *R. cymbalaria* and *L. schaffneriana*; *G. fluitans* in Cm; and *J. arcticus* in Cc. For other species, this pattern was reversed. *E. acicularis* was more abundant in the 5-10cm depth than in the 0-5cm depth in all marshes, whereas in Cg, it was *R. pinnata* and *J. tenuis* in Cc (Table 1).

Established vegetation and seed bank: The first two DCA axes accounted for 98% of the total variance of the data (Fig. 4). The first axis in the ordination diagram shows a clear separation between the records of the established vegetation and total seed bank, whereas the second axis makes a separation among the three marshes studied (Fig. 4). Species diversity was significantly less in the vegetation than in the seed bank (Fig. 2, Table 1). Of the 61 seed-bank species, only 25 (41%) were found in vegetation, and of the 49 species of established vegetation, 24 (49%) were not present in the seed bank.

Half or more of the species that germinated from the seed bank of Cg (50%), Cm (70%), and Cc (65%) were not observed in the established vegetation of each wetland. The average species similarity between the established vegetation and the seed bank of the three marshes was 39%. Cg had the highest species similarity between established vegetation and seed bank (48%, Table 2), 12 species were common between the two flora (Table 1), and only *L. schaffneriana* (r=0.55, p<0.05) and *R. cymbalaria* (r=0.67, p<0.05) showed a significant relationship between the abundance of the total seed bank and the emergent community. The floristic similarity between the vegetation and seed bank was low in Cc (34%) and Cm (35%, Table 2), and no species was significantly correlated between the total seed bank and established vegetation.

Some species were more abundant in the vegetation than in the seed bank (Table 1), such as *M. heterophyllum* in Cc and *J. bellidiflora* in Cm. Other species were more abundant in the

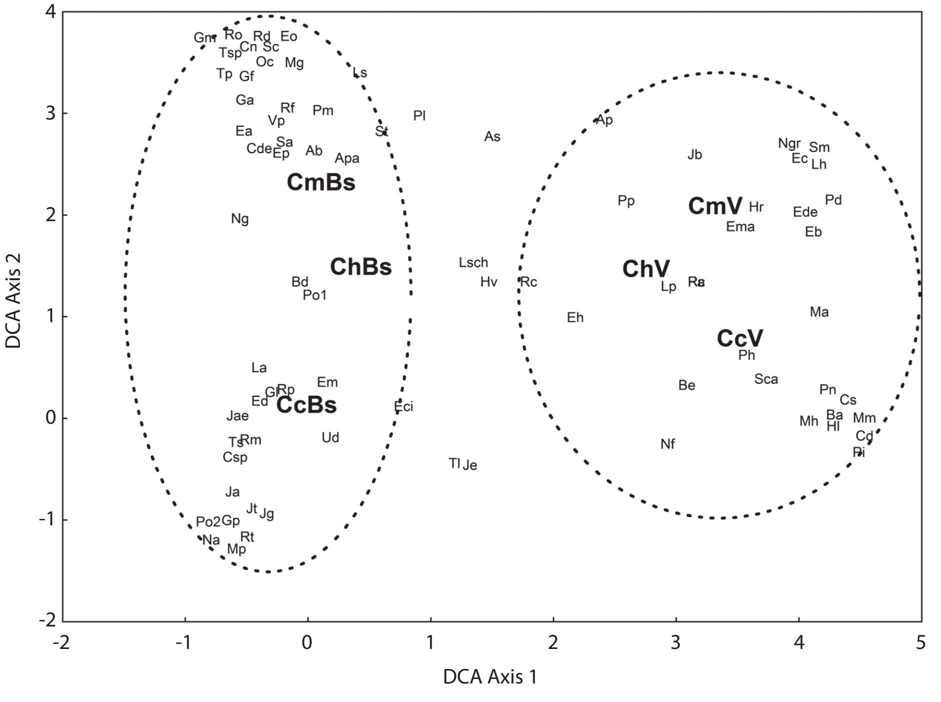

Fig. 4. Ordination for the first two axes of the detrended correspondence analysis (DCA). This shows the relative position of the vegetation coverage and total seed bank density in the Lerma marshes. The eigenvalues of axis 1 and 2 are 0.71 and 0.27. CgV, CmV, and CcV represent the established vegetation and CgSb, CmSb, and CcSb the total seed bank of each marsh (Cg=Chignahuapan, Cm=Chimaliapan, Cc=Chiconahuapa). Bold letters indicate the centroid of each marsh. For species abbreviations see table 1.

seed bank than in the vegetation. *Rorippa pinnata* was more abundant and frequent in the Cg seed bank but was rare in the established vegetation. For others, the species were only found in the vegetation or in the seed bank, such as *E. acicularis* and *G. fluitans* that emerged frequently in the Cm seed bank but were absent in the vegetation. Similarly, *J. arcticus* and *J. tenuis* had a high density in the Cc seed bank but did not appear in its vegetation. The opposite was true for *E. macrostachya*, *P. annua*, *S. macrophylla,* and *S. californicus*, which occurred frequently in the wetlands vegetation, but were not detected in seed banks (Table 1).

The life-forms analysis showed that perennial herbs, and particularly rooted emergent hydrophytes (REH), dominated in all three wetlands, but their percentage in both established vegetation and in the seed bank differed significantly among the three marshes (Table 4). The percentage of flood-tolerant species of established vegetation was significantly higher in Cg than in the other two marshes; nevertheless, in the seed bank, the opposite was found (Table 4). Cc had the highest proportion of perennial species and life-forms, both of established vegetation and in the seed bank (Table 4).

TABLE 4
Life-form percentage of total seed bank and established vegetation of the Lerma marshes

	Seed bank			Vegetation		
	Cg	Cm	Cc	Cg	Cm	Cc
Annual	48	41	33	27	22	7
Perennial	52	59	67	73	78	93
TT	3^{a}	7^{b}	7^{b}	17^{a}	13^{b}	5^{c}
REH	96^{a}	92^{b}	89^{b}	83^{a}	79^{b}	49^{c}
RSH			2			31
EHFL			1		3^{a}	5^{a}
EHPS	1^{a}	1^{a}	1^{a}		1^{a}	5^{b}
FFH					4^{a}	5^{a}
FSH						1

Cg=Chignahuapan, Cm=Chimaliapan, Cc=Chiconahuapa, TT=tolerant terrestrial plant, REH=rooted emergent hydrophytes, RSH=rooted submerged hydrophytes, EHFL=emergent hydrophytes with floating leaves, EHPS=emergent hydrophytes with prostrate stems, FFH=free floating hydrophytes, FSH=free submerged hydrophytes. Different letters indicate statistical significance of the differences (Mann-Whitney test, $p<0.05$).

DISCUSSION

This study examined differences in the floristic composition and diversity of standing vegetation and the seed bank in the Lerma marshes. The vegetation diversity of the wetlands showed significant differences. Cc was the most diverse marsh. However, the Cc vegetation was similar to Cm rather than the Cg vegetation. This similarity is based on a qualitative index; a different grouping might occur with a quantitative index. The similarity found here between the Cc and Cm vegetation could be caused by similar topographic and soil conditions, but the most important reason could be the water depth and its permanence in areas of emergent vegetation of both marshes.

Cm and Cc water levels are 1m to 1.5m deep in the rainy season and slightly less than 90cm in the dry season. In contrast, the average water level in Cg is less than 60cm deep in the rainy season and decreases dramatically in the dry season, so the soil is saturated with water for only four to six months. The disturbances associated with these water-level fluctuations (natural or anthropogenic) are recognized as sources of change in the composition and distribution of aquatic plant communities (van der Valk, 1981; Chang et al., 2001). Although this study did not directly assess the spatial and temporal variations of the water level, seasonal changes of this resource may explain the low diversity in the Cg life-forms, species richness, and the increased terrestrial species tolerant to flooding, in both the vegetation and seed bank.

The diversity of the Lerma marshes is important and high because it retains many of the typical wetland elements of central Mexico, with some endemic species such as *Sagittaria macrophylla*, *Jaegeria bellidiflora*, *Jaegeria glabra*, *Euphrosyne partheniifolia*, *Nymphaea gracilis* Zucc.*,* and *Glyceria mexicana* (Kelso) Beetle. However, the presence of aquatic weeds and terrestrial plants tolerant to flooding suggests the continued deterioration of the marshes.

Overall, the Lerma marshes have diverse seed banks (61 species), and they are abundant (27 000±4 000seeds/m^2 on average). Individually, species richness and the density per square meter of seeds from each marsh are within the range reported for freshwater wetlands of North America (van der Valk & Davis, 1976, 1978, 1979; Leck & Graveline, 1979; Leck & Simpson, 1987) or elsewhere (Gordon, 2000; Lui et al., 2005; Liu, Zhang, & Lui, 2009; Aponte, Kazakis, Ghosn, & Papanastasis, 2010), where there are 23 to 59 species (Leck, 1989) and from 200 (Liu et al., 2009) to 256 000seeds/m^2 (van der Valk & Davis, 1979). The species richness and average density of seeds found in the marshes differ significantly among them. The greatest densities of seedlings were found in the Cg seed bank, whereas the Cm seed bank was the richest. Despite these differences, on the community level, the seed banks of Cm and Cg are more alike because they share more species. The dissimilarity of the Cc seed bank with the two other marshes can be attributed mainly to the presence of rare species (Frequency <20%).

Each wetland had two abundant plant species in the seed bank. The overrepresentation of one to a few species in the seed bank is a common feature in wetlands (Harper, 1977), including salt marshes (Hopkins & Parker, 1984), coastal areas (Pierce & Cowling, 1991), and temporary ponds (Aponte et al., 2010), in which from 15% to 90% of the seed bank may be dominated by graminoids (Leck, 1989). In each Lerma marsh, more than 24% of the seed density was concentrated in two different species (six in total) of which four were graminoids. The dominance of these species can be explained by their rapid production of seeds, by the large number of seeds remaining in the sediment that are tolerant of some perturbations, and by the fact that they are long-lived seeds (Matus, Papp, & Tothmeresz, 2005). These are strategies for plants that die each season and that are replaced annually during favorable periods (Thompson & Grime, 1979). There are two species belonging to this group in Cc, *Juncus arcticus* and *Juncus tenuis*, which are characterized by forming a persistent and abundant seed bank, though in the established vegetation they are underrepresented (Leck, 1989; Wilson et al., 1993).

Seed density differed among marshes and sediment depths (0-5 and 5-10cm). In Cm and Cg, the seed number per square meter and the seed-bank species richness decreased with sediment depth. Over 50% of the species found at both depths were more abundant near the surface. This phenomenon has been documented for various environments, especially in water bodies (Leck & Graveline, 1979; van der Valk & Davis, 1979; Leck & Simpson, 1987; Raffaele, 1996; Boedeltje, Baker, & Heerdt, 2003), and has been linked with the ability of seeds to penetrate the soil (Thompson, Band, & Hodgson, 1993), with the greatest effect of the seed rain in the sediment surface (Poschlod & Jackel, 1993), and with the effect of disturbances caused by animals (Bonis & Lepart, 1994). Around the Lerma marshes, livestock and ducks are common; we observed foraging inward of the marshes. Trampling by livestock is the most important cause of sediment disturbance, and ducks (particularly seed-eating species) can also disturb the top few centimeters of sediment when searching for food (Bonis & Lepart, 1994). The effects of such disturbances should be evaluated in the study area because they can modify the seed bank distributions.

The composition of the seed bank of each marsh and the differences among the marshes and sediment may be useful in determining the potential for the recovery of plant communities in the area and suggest that, in each area, there are environmental factors that may be affecting their diversity.

The data show low similarity between the vegetation and seed banks of the Lerma marshes. Compared with the other two marshes, Cg was characterized by a high seed density (especially in the upper sediment layer), greater similarity between the seed bank and vegetation, and low species diversity in the established vegetation and seed bank. This is associated with the presence of a greater number of annual species in the Cg vegetation (Chambers, 1993) and suggests that they form a persistent seed bank. The presence of annual plants in saline (Ungar & Woodell, 1996b; Bossuyt & Honnay, 2008) and freshwater wetlands (Middleton, 2003) is favored by their ability to tolerate natural and anthropogenic disturbance and to produce a large amount of long-lived seeds (van der Valk & Davis, 1978; Matus et al., 2005; Brock, 2011). The seeds of these species remain viable in the soil, awaiting favorable conditions for germination (Egan & Ungar, 2000), so they are the potential reserve that can be expressed after a disturbance.

Previous studies have found that species abundant in the established vegetation are often uncommon or absent in the seed bank (Leck & Simpson, 1987; Poiani & Dixon, 1995; Liu et al., 2009). In the Lerma marshes, we found the same phenomenon. The ten species with the highest coverage in the vegetation of the three marshes had few seeds in the seed bank, and some were completely absent. One explanation for this may be the presence of dormant seeds, nonviable seeds, or unfavorable conditions for germination (Leck, 1989), and therefore, they were not detected by the germination method. Another explanation for this low similarity may be partly caused by the dominance of rhizomatous perennials whose contribution to the seed bank is low because they have a greater investment in clonal growth (Diemer & Prock, 1993). The last explanation may clarify the low similarities between the established vegetation and the seed bank in Cc and Cm.

Not only those plants with high coverage are underrepresented in the seed bank. It appears that the abundance of established vegetation is irrelevant to presence in the seed bank. Considering the species found in the established vegetation and seed bank for Cg (12), Cm (13), and Cc (11), only *Ranunculus cymbalaria* and *Lilaeopsis schaffneriana* showed a relatively high and positive correlation between seedling density and vegetation abundance.

The low correlation between the vegetation and the seed bank appears to be a recurring phenomenon in several aquatic environments (Ungar & Woodell, 1996a; Egan & Ungar, 2000; Liu et al., 2009) and provides evidence that the seed bank may have limited importance in the development, structure, and composition of the plant community (Gordon, 2000). In the Lerma marshes, many abundant species in the established vegetation are absent or have low density in the seed bank, so the chances of natural regeneration of these communities from the seed bank are reduced.

Over 50% of the species that germinated from the seed bank were not recognized in the current Lerma marsh vegetation. The seeds may have come from neighboring communities and therefore did not originate in the wetlands, but it is also likely that their absence was because current conditions are limiting their establishment. The largest components of the seed bank in the Lerma marshes were the emergent hydrophytes and tolerant terrestrials. Considering the environmental heterogeneity, their low presence in the vegetation can be associated with their germination, usually during low flood conditions (van der Valk & Davis, 1978; van der Valk, 1981). One might expect that this fraction of the seed bank, especially those seeds with greater abundance, arises in the marsh as a consequence of some disturbance that gives rise to conditions favorable to the germination of species from a diverse seed bank reservoir (Brock & Rogers, 1998). However, it is also possible that after a disturbance, some opportunistic species germinate from the seed bank. Among these are nonnative invasives, and their occurrence may be an important warning for managers of these areas because the presence of opportunistic species can lead to competition and exclusion of the natural wetlands species.

Another factor that may determine the differences between the seed bank and vegetation, is the zoochory by the cattle present in some areas of the Lerma wetlands, which may be causing the entry of seeds that are not in the marshes' vegetation. The dissimilarity between the seed bank and vegetation was probably increased by the large number of rare species present only in the seed bank or in vegetation

(Amiaud & Touzard, 2004). Coverage and sampling time can also lead to discrepancies between the vegetation and seed bank, especially in seasonal environments, where species phenology and life cycles are associated with seasonal changes.

The large variation in seed bank and wetland vegetation around the world makes comparison difficult, especially because the wetland plant community and seed bank dynamics are directly related to specific environmental changes (van der Valk & Davis, 1978; van der Valk, 1981) and often from the impact of human activities, which are different in each part of the world. However, comparative regional studies allow a better understanding of the dynamics of water bodies and may guide activities related to their management and conservation (Leck & Brock, 2000; Lui et al., 2005; Brock, 2011). Anecdotal reports indicate that in the pre-Hispanic era (five centuries ago), the marshes formed a single wetland, although when this area became fragmented is unknown. The species richness before this fragmentation is also undetermined. Currently, each marsh has a different assemblage of species, both in the established vegetation and in its seed bank. Cc was the most diverse marsh even though it has the smallest surface area. The dominance of a few species and the presence of opportunistic land plants indicate wetland degradation, which is the product of both the historical and the current regime of disturbance to which it is subjected (Zepeda et al., 2012a). Actually, the marshes are part of a suburban area with an intense disturbance regime due to the presence of human production activities. To ensure the permanence of these marshes, their biodiversity, and therefore the environmental services they provide will require planning and efforts to control and monitor hydrology, water quality, and the influence of human activities.

Knowledge of the spatial and temporal dynamics of the seed bank and established vegetation in the Lerma marshes are essential in order to assess the potential for restoration of the wetlands, because they enable predictions of the community structure of aquatic plants and their response to disturbance (Cronk & Fennessy, 2001). This also facilitates the establishment of preservation priorities for native and noninvasive aquatic species those are currently scarce or absent in the vegetation, but which are historically relevant in the dynamics of the wetland.

ACKNOWLEDGMENTS

Special thanks to anonymous referees for their critical comments and helpful suggestions for improving the manuscript. Thanks also to the Universidad Autónoma del Estado de México and to Consejo Mexiquense de la Ciencia y la Tecnología for financial support. Thanks to Itzi Bautista and David Colón Quezada for their help in the sampling and to Omar Franco Mora for permitting us to use the greenhouse.

RESUMEN

Los bancos de semillas desempeñan un papel central en la dinámica de la vegetación de muchos humedales. Por lo tanto, el conocimiento de los depósitos de semillas en los suelos de las comunidades acuáticas debe proporcionar herramientas útiles para los esfuerzos de conservación y restauración. Este estudio se llevó a cabo en las ciénegas de Lerma, uno de los últimos vestigios de las grandes zonas inundadas que antes cubrían la Meseta Central Mexicana. El objetivo principal fue determinar la composición y abundancia de los bancos de semillas y su relación con la vegetación establecida en las tres ciénegas de Lerma. En cada humedal se seleccionaron sistemáticamente de 18 a 40 sitios de muestreo. En cada sitio se colocaron dos líneas de 10m perpendiculares a la orilla sobre las que se evaluó la composición y cobertura de plantas vasculares a intervalos de 0.5m. En los sitios de muestreo donde se evaluó la vegetación establecida, se recolectó una muestra de los 10cm superiores de sedimento y se separó en una capa superior (0 a 5cm) y otra inferior (5-10cm). Estas muestras se utilizaron para evaluar el banco de semillas por el método de emergencia de plántulas. Todas las muestras se colocaron en un invernadero a 20-25ºC y se mantuvieron inundadas durante 15 semanas. Cuarenta y nueve especies se registraron en la vegetación. Chiconahuapan presentó la flora más rica y diversas, así como el mayor número de especies perennes. El análisis de las formas de vida mostró que las hierbas perennes y especialmente las hidrófitas arraigada emergente dominaron en los tres humedales. Sesenta y un especies se identificaron en el banco de semillas total, Chimaliapan presentó el banco de semillas total más diverso, mientras que la densidad promedio de plántulas fue mayor

en Chignahuapan. Sólo dos especies de todo el banco de semillas de cada ciénega presentaron una densidad mayor del 10% del total y más de la mitad de las especies fueron poco frecuentes. La capa superior de sedimentos (0-5cm) exhibió dos veces más semillas/m^2 y especies por muestra que la capa inferior (5-10cm), se observó una disminución significativa de la densidad de semillas con la profundidad. El análisis de correspondencia sin tendencia produjo una separación clara entre la composición de los bancos de semillas y la de la vegetación establecida. En general, en cada ciénega hay menos diversidad de especies en la vegetación establecida que en el banco de semillas. El dominio de pocas especies en el banco de semillas, la presencia de especies oportunistas y la escasa representación de las plantas establecidas en el banco de semillas sugiere degradación de los humedales y una baja probabilidad de regeneración de las comunidades naturales desde el banco de semillas. Para garantizar la permanencia de estos sistemas, su biodiversidad y por tanto los servicios ambientales que ofrecen, se requiere de esfuerzos para controlar y supervisar la hidrología y la influencia de las actividades humanas.

Palabras clave: Chignahuapan, diversidad de humedales, flora, hidrófitas, México, humedales degradados, restauración de humedales, cuenca alta del río Lerma.

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