

The influence of water level and salinity on plant assemblages of a seasonally flooded Mediterranean wetland

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Abstract We studied the key environmental variables shaping plant assemblages in Mediterranean abandoned ricefields with contrasting freshwater inputs over saline sediments. Plant species cover, water levels and soil variables were studied following a stratified random sampling design. Multivariate analysis identified water regime, particularly summer and autumn irrigation, as the most important environmental variable associated with vegetation composition. Distribution of annual and emergent macrophytes was not associated to salinity as found at the study site (0.57–4.1 mS/cm). Increased soil salinity, caused by summer irrigation near the soil surface did affect shallow-marsh assemblage distribution. These key environmental characteristics allowed us to identify six main assemblages. Annual macrophytes (such as *Zannichellia palustris*) were defined by high (over 10 cm) annual mean water level (MWL) and early successional conditions; emergent macrophytes (such as *Typha* spp.,

Scirpus lacustris) by annual MWL of 10 to –25 cm and continuous shallow flooding in summer and autumn (MWL of 0–10 cm). The shallow-marsh group, correlated with annual MWL –25 to –100 cm, separated into two subgroups by salinity: grassland (including *Paspalum distichum*) with summer and autumn MWL below –25 cm and brackish (with *Juncus subulatus* or *Agrostis stolonifera*) with summer and autumn MWL just below the soil surface (0 to –25 cm). Water levels for the grassland subgroup may equate with a salinity ‘refuge’ for *P. distichum*. Time was a further determinant of variation in the full data set. Abundance of a large group of agricultural annuals (such as *Sonchus tenerrimus*) and damp ground annuals (including ricefield weeds such as *Ammannia robusta*) decreased with time as bare ground disappeared. Maintenance of spatial vegetation heterogeneity in abandoned ricefields is contingent on continued water regime management.

Keywords Macrophytes · Mediterranean wetlands · Multivariate analysis · Plant assemblages · Salinity · Water regime

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Introduction

Water regime (depth, duration and frequency of flooding) is the principal factor determining

plant species distribution along the land-water interface in wetlands (Mitsch and Gosselink 1993). Spatial heterogeneity in wetland vegetation is conditioned by diverse factors including soil composition and microclimate, but in particular topography through its controlling influence on water regime (Jenny 1980; Keddy 1984; Shay and Shay 1986). Abandoned ricefields play an important role in mitigating wetland loss in the Mediterranean (Vaqué et al. 1989; Mesléard 1994; Sargatal 1995; Comin et al. 1997) and water management may often continue for wildlife although cultivation has ceased. The abandoned ricefield parcels retain the topographical homogeneity and water channel systems engineered to enable rice production.

Establishing the water regime conditioning wetland plant assemblages is complex given that these often fluctuate within a year and from year to year. For instance, general descriptions of water regime such as “limosal ecophase; – 15 to + 30 cm for most of the year” have been used to detail Moravian reedswamp communities (Fiala and Kêt 1971), the period of sediment exposure (e.g. “early to mid-June”, Harris and Marshall 1963) to describe northern US marsh communities, and “shallow-marsh” for Saskatchewan slough vegetation (Millar 1973; Walker and Coupland 1970). More recently, mean water table levels in June best explained species distribution along a lakeshore coenocline in Norway (Odland and del Moral 2002). However, there are few studies detailing the water levels conditioning plant assemblages at the land-water interface of Mediterranean wetlands. Research on abandoned ricefields in the Camargue (southern France) uses broad water management categories (“summer or winter flooding”; Mesléard et al. 1995).

Temporal variation in wetland plant assemblage composition is influenced by diverse factors, including disturbance and water regime. Water levels affect plant recruitment and Seabloom et al. (1998) suggested that water-depth sorts seedlings according to adult water-depth tolerances. Duration of flooding events was found to be important in segregating wetland communities at establishment in New South Wales (Casanova and Brock 2000). Keddy and Ellis (1985) found

disturbance such as fluctuating water levels and waves minimised the value of specialisation on a narrow range of heights leading to broad tolerance limits (over a – 5 to + 10 cm gradient) for water level in the recruitment phase. Likewise, Chambers and McComb (1994) found optimum water-depth for establishment was broad, in the range 0–10 cm.

Salinity also plays a part in shaping plant assemblages where freshwater inputs occur over saline soils (Shay and Shay 1986; Kadlec 1982; Walker and Coupland 1968, 1970; Bolen 1964). Kadlec (1982) reported spatial distribution of emergent vegetation of Salt Lake marshes was not affected by sediment salinities up to 16 mS/cm, but this was subsequently refined (Kadlec and Smith 1989) in line with Bolen (1964), who reported sediment salinities around 10 mS/cm responsible for competitive superiority of *Scirpus olneyi* over *S. acutus* and *Typha* spp. This knowledge underpins recommended techniques for habitat management of undesirable species (mainly *Typha* spp.) in Great Salt Lake spring-fed saltmarshes (Kadlec and Smith 1989); brackish South Atlantic coastal marshes (Gordon et al. 1989) and Northern Great Plains saline basins (Pederson et al. 1989). Although Mesléard et al. (1991) showed that winter or summer freshwater flooding is needed to prevent abandoned Mediterranean ricefields reverting to saltmarsh, details of the interactive effects of water levels and salinity on plant assemblages in the Mediterranean region are lacking.

The objectives of this study are to analyse the relationship between key environmental variables and vegetation composition in abandoned Mediterranean ricefields and to compare the relative roles of water regime and soil variables, particularly salinity, in shaping the plant assemblages. Six different assemblages are described and related to environmental variables. These abandoned ricefields are located in a Natural Park and our findings have already been applied to enhance vegetation heterogeneity and the populations of endangered birds. The management implications for similar habitats in Mediterranean wetlands are briefly indicated.

Methods

Study area

The study area were the wetlands in the Aiguamolls de l'Empordà Natural Park (Girona, NE Spain). The climate is typically Mediterranean with hot, dry summers (mean 23.7°C in July and 8.6°C in January) and an annual evapotranspiration deficit exceeding 600 mm. Mean annual precipitation is 712 mm and during the study period (from 1995 to 1998) rainfall fluctuated between 433 and 833 mm. The wetlands sit on degraded saltmarsh formed by silting up of coastal lagoons during the Holocene. Sediments consist of a surface layer (ca. 40 m) of silt and clay deposited over medium and fine sand that acts as an aquifer (Bach 1990). An active subterranean circulation of fresh and saline water (Quintana et al. 1998) gives large oscillations in water levels between seasons (1–1.5 m below the surface in summer to ca. 20 cm in winter) and aquifer water

conductivities ranging from 0.5 to 5.7 mS/cm (Bach 1990; Mas-Pla 1999).

Study site

The study site (Al Matà) was 18 ha of abandoned ricefields within the Alt Empordà wetlands, 1.5 km from the present coastline. The ricefields were created in 1948 and cultivated intermittently until 1994, when cultivation ceased. The ricefields retain the engineered topographical homogeneity and water channels, but some peripheral channels were deepened in 1994 to attract birds (referred to as “canals”) and topsoil was removed from one parcel to construct a track. The study period ran from 1995 to 1998 (inclusive).

The existing ricefield divisions gave 11 main parcels and 6 main canals at the study site (see Fig. 1). One parcel and the six canals had topsoil removed. In each main parcel 20 × 30 m blocks were marked out, giving a total of 41 blocks (see Fig. 1). Only parcels with a uniform surface, level

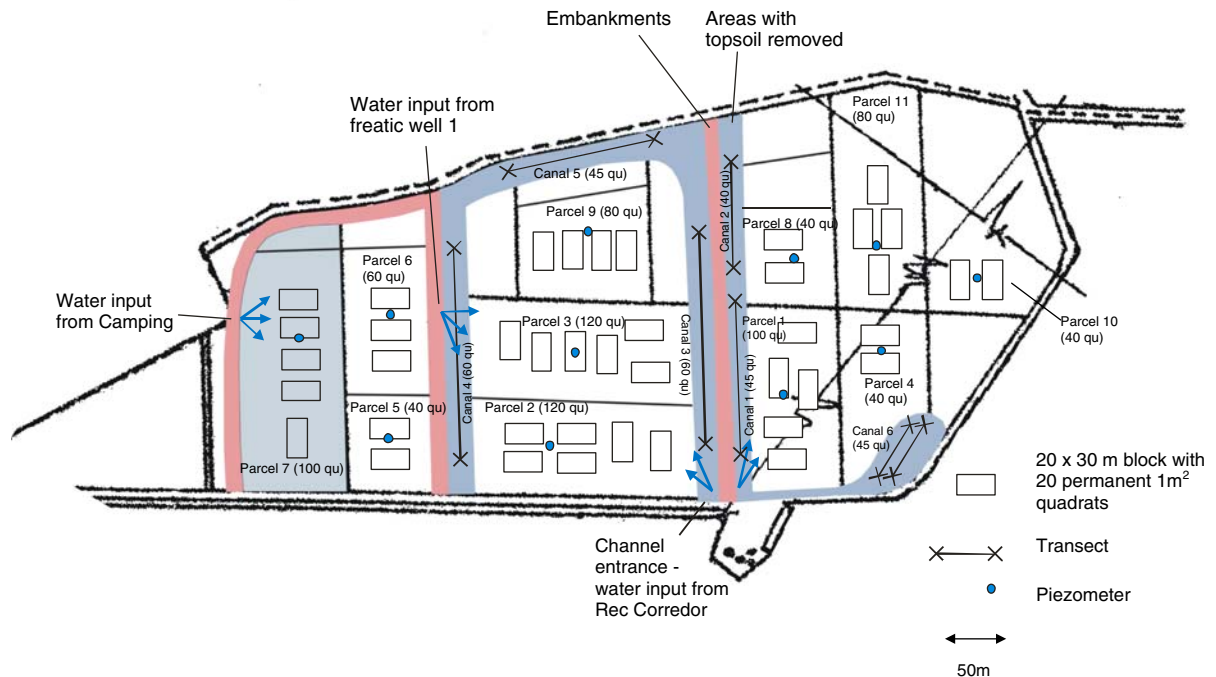


Fig. 1 Map of the study site (Al Matà abandoned ricefields) showing layout of the ricefield parcels and canals and the study blocks and transects

and water management were chosen and edges were avoided when placing blocks. Within each block, 20 permanent 1 m² quadrats were located using a grid and random coordinates, giving 820 permanent quadrats. The narrow width of the canals meant block sampling was not appropriate so transects, avoiding the edges, were set up and quadrats sampled at random intervals, giving a total of 295 quadrats. The height of the parcels with respect to sea level (to the nearest meter) were determined by a topographer.

Water management in the ricefields since abandonment in 1994

Although rice-growing ceased in 1994, water levels are still managed in the abandoned ricefields to enhance bird populations. Water levels in the parcels depend on freshwater inputs via an irrigation channel (in addition to natural rainfall inputs). Water was pumped (flow permitting) to manage levels through the dry season and from April to September 1995 to 1997 (inclusive) were maintained up to 20 cm in parcels nearer the channel entrance and up to 32 cm in the excavated canals. The underlying pattern of water level fluctuation in parcels further from the channel entrance was higher in winter and spring and lower in summer and autumn. Levels in the central parcels, near the channel entrance, were also boosted by irrigation from a freatic well (summer 1995 to July 1997). Two parcels received excess water from a lagoonal treatment system after 31 July 1997. Water management ceased in June 1998 due to low rainfall. This caused abrupt changes in the vegetation.

Mean conductivity of water from the channel was 0.82 mS/cm (maximum 1.30 mS/cm), with higher values recorded inside the ricefields through evaporation (2.35 mS/cm in August) (Ribas-de-Pouplana et al. 1986; Consorci de la Costa Brava 1998). Channel water had 86.3 mg/l of phosphorous concentration and very high levels of dissolved inorganic nitrogen (8.5 mg/l) (Consorci de la Costa Brava 1998). Water from the freatic well used to irrigate the study parcels in summer had a conductivity of 1.71 mS/cm and that from the lagoonal treatment system, 3.15 mS/cm.

Field measurements

The study period ran from 1995 to 1998 (inclusive). A piezometer to 1 m was established at the centre of each parcel. Water levels were taken monthly in winter, fortnightly in spring and autumn and weekly in summer, a regime chosen to fit the characteristics of the Mediterranean wetland (e.g. Bach 1990; Quintana et al. 1998). Levels were measured on 66 days between March 1995 and February 1999. Only data to the end of August 1998 were used for analysis (60 readings). Mean water levels (MWL) were calculated in spring (March–May), summer (June to August), autumn (September to November), winter (December–February), and annual (September–August). Water samples from the freatic well were kept at 5°C until conductivity was measured in the laboratory.

Soil samples at 15 and 30 cm were taken twice yearly (at the end of April and July) from each parcel. This represented the start and end of the growing season for most of the vegetation studied. Samples were dried thoroughly at room temperature, passed through a 2 mm sieve, and then analysed following standard laboratory procedures for conductivity, organic matter, texture, and pH. Cover of all vascular species and algae was recorded for each quadrat in July and August from 1995 to 1998 (inclusive). Percentage cover was recorded, using a 1 m² quadrat subdivided to 0.0625 m². Species of note are in the Girona University herbarium. Nomenclature followed Bolòs and Vigo (1984).

Data analysis

The ecology of the assemblages was studied using ordination techniques, which arrange the species and sites by similarity in a few axes that summarise most of the information in the data matrix. Canonical correspondence analysis (CCA) was used to analyse the matrix of species abundance (Fig. 3). Detrended correspondence analysis (DCA) showed a gradient length of 4.3 SD, suggesting a long environmental gradient and the use of unimodal response models (ter Braak and Smilauer 1998; ter Braak and Prentice 1988; ter Braak and Looman 1986). The use of a series of

ordinations allowed us to focus on particular aspects of the data. Canals formed an important part of the variation along DCA Axis 1 and were removed from the dataset for analysis shown as Figs. 5–7; for Fig. 7 all topsoil removed data (canals and Parcel 7) were excluded allowing detailed analysis of the grassland assemblage. The shortened gradient in these analyses suggested that ordination techniques based on linear species response models [Principal components analysis (PCA) and Redundancy analysis (RA)] would be more appropriate. Partial ordination allows the effect of particular environmental variables to be singled out from variation associated with other variables and thereby “partialled out” as covariates (Jongman et al. 1995). This was used to factor out variation due to successional processes in time, by entering the years as covariates (Figs. 4, 7). Multiple linear regression models were developed by stepwise selection of independent variables. R^2 is the adjusted value for models with more than one independent variable. Analyses were carried out using CANOCO 4.0 (ter Braak and Smilauer 1998) and SPSS 7.5.

Results

Variation in physical parameters

Mean water levels at the site ranged from -1.6 to 30.3 cm in winter, -11 to 29 cm in spring, -79 to 20 cm in summer, -65.3 to 25.3 cm in autumn and annually from 28 to -48 cm. Annual MWL was most strongly correlated with summer MWL. Examples of water level patterns are shown in Fig. 2: parcels further from the central channel entrance following more seasonal water fluctuations (Fig. 2a); central parcels nearest the channel entrance also receiving additional irrigation from the freatic well flooding during the dry season (Fig. 2b) and the canals (Fig. 2c).

Soil conductivity ranged from 0.57 mS/cm (0.366 g/l NaCl) to 4.1 mS/cm (2.02 g/l NaCl). Values were significantly higher at 10 cm than 30 cm ($t_{32} = 7.47$, $P < 0.0001$). Surface salinity in May and August was explained by summer and autumn irrigation, increasing with time (e.g. August $R^2 = 0.44$; $P < 0.0005$). Subsoil salinities

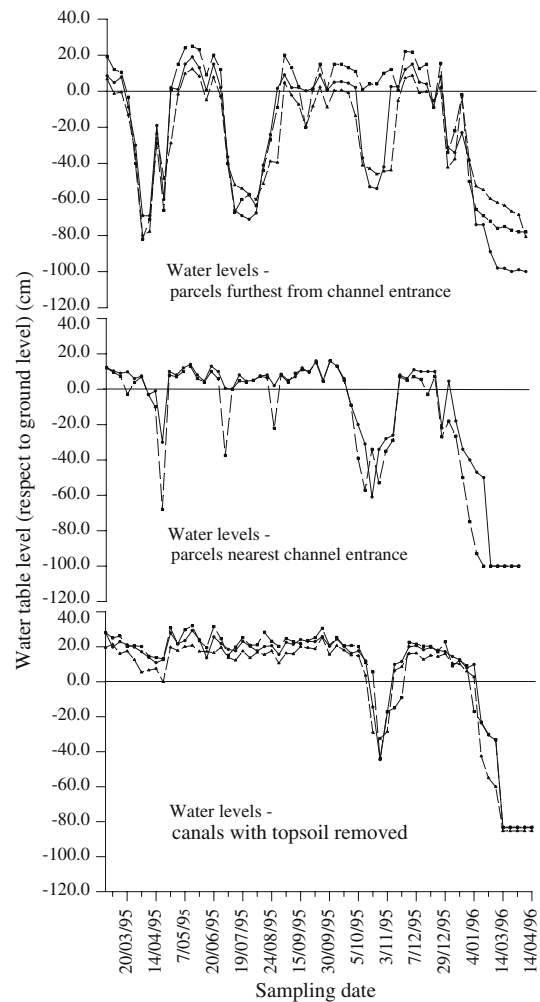


Fig. 2 Water levels from 20 March 1995 to 28 August 1998 in: (a) three parcels furthest from channel entrance with seasonal water fluctuations (parcels 5, 6 and 7) (b) two central parcels, near the channel entrance (parcels 2 and 3); and (c) three canals (topsoil removed) (canals 3, 4 and 5). Parcel 7 received excess water from a lagoonal treatment system after 31 July 1997. The two central parcels received additional irrigation from a well during summer. Note the abrupt change in management in summer 1998

were similarly explained by autumn irrigation, with the effect increasing with time (e.g. in May $R^2 = 0.436$; $P < 0.0005$). Spearman correlation coefficients showed the strongest link with salinity to be with water level classes near the surface (from 10 cm through to -25 cm), e.g. salinity at 30 cm in May and class 0 to -25 cm; 0.511 ; $P < 0.05$); likewise salinity was highly negatively

correlated to autumn water levels below -25 cm (salinity at 10 cm in August and class -50 to -100 cm; $R^2 = 0.580$; $P < 0.05$). Flooding in autumn increased organic matter build up in the lower soil section (at 30 cm) (e.g. $R^2 = 0.425$; $P < 0.0005$ for organic matter in May and autumn irrigation). The commonest soil textures were clay-loam and silt-clay-loam. Topsoil removal increased total sand and decreased clay.

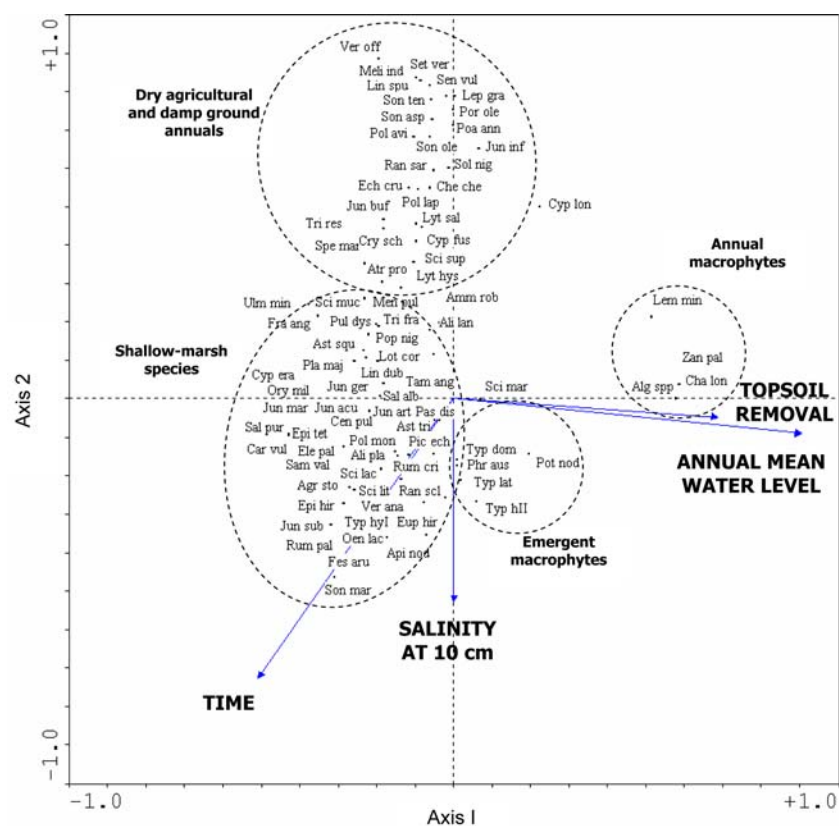
The effects of environmental variables on vegetation

The first two axis of a CCA of the full dataset with all the measured environmental variables (MWL, time, topsoil removal, salinity at 10 cm in May (log-transformed), and OM at 30 cm in May (log-transformed) explained 67.9% of the variance in species composition. The first axis (Fig. 3) was related to annual MWL and to topsoil removal. This clearly separated the annual macrophytes (e.g. *Zannichellia palustris*, *Chara* spp.) and the

emergent macrophytes (*Typha latifolia*, *T. dominguisensis* and *Typha* hybrids) from a large group of perennial shallow-marsh species (*Juncus gerardi*, *Rumex palustris* or *Carex vulpina*) to the left of the figure (see Appendix 1 for mean species cover values and acronyms used in ordination plots). Variation along the second axis was a function of time since abandonment and separated the agricultural annual “weeds”, abundant in years 1 and 2 (*Solanum nigrum*, *Sonchus asper*, *Linaria spuria*, *Polygonum lapathifolium*, *Echinochloa crus-galli*) from the large group of perennials whose abundance increased with time (*Agrostis stolonifera*, *Tamarix anglica*, *Juncus* spp., *Eleocharis palustris*). Axis 2 was also a gradient of increasing soil salinity and organic matter caused by summer irrigation, separating perennials such as *Salix alba*, *Populus alba* or *Plantago major* (less salinity) from *Euphorbia hirsuta*, *Rumex palustris* or *Juncus subulatus*.

The first axis eigenvalues for DCA (analysis not shown) and CCA (0.58 and 0.46, respectively)

Fig. 3 Canonical correspondence analysis (CCA) biplot of the full data set (species cover square-root transformed). Eigenvalues = 0.383 and 0.293; species–environment correlations = 0.844 and 0.857; and cumulative percentage variance of species–environment relation = 38.5 and 67.9%, for the first two axes respectively. Total inertia = 2.902; sum of all unconstrained eigenvalues = 2.902, sum of all canonical eigenvalues = 0.995



were similar and larger than the rest, suggesting that the measured environmental variables adequately explained the major variation in plant species composition (Jongman et al. 1995; Palmer 1998). This was confirmed by inputting the environmental variables as covariates and performing an indirect gradient analysis on the residual variation as a further check (Palmer 1998; ter Braak and Prentice 1988). The species assemblages were then described using four water level classes (Fig. 4). The first two RA axes explained 79.5% of the variance in species composition. Annual macrophytes were strongly correlated with high annual MWL over 10 cm and topsoil removal, associated particularly with the canals. The emergent macrophytes such as *Typha* spp. or *Scirpus lacustris* highly correlated with annual MWL ranging from 10 to –25 cm and the large “shallow-marsh” group from –25 to –100 cm, with the –25 to –50 cm annual MWL vector falling centrally to this group.

Seasonal water level classes were used to give more detail of the assemblages (Fig. 5). The first

two RA axes explained 70.2% of the variance in species composition. Shallow flooding in summer and autumn (water levels from 0 to 10 cm) will give emergent macrophytes (such as *Typha* spp. or *S. lacustris*) while summer water levels below 25 cm are the major determinant for the shallow-marsh group including *Juncus* spp., *Eleocharis palustris*, *Plantago major*, *Agrostis stolonifera*, *Paspalum distichum*, and *Salix purpurea*. The link between autumn irrigation near the surface and salinity is clear. This analysis (with canals omitted) showed how *Zannichellia palustris* and *Chara* spp. were also found on two parcels shallowly irrigated throughout summer and autumn (first 2 years only). The large group of annuals associated with the first year of abandonment includes dry agricultural weeds, damp ground specialists, and ricefield weeds.

To detail the ecological differences within the large shallow-marsh group, the main parcels (excluding topsoil removal data) were studied (Fig. 6; Table 1). The first PCA axis corresponded to a gradient of summer irrigation and

Fig. 4 Partial redundancy analysis biplot with years as covariates and annual mean water level (MWL) as classes. Other input variables were topsoil removal, salinity at 10 cm in May (log-transformed), and OM at 30 cm in May (log-transformed). Eigenvalues = 0.129 and 0.070; species–environment correlations = 0.779 and 0.544; and cumulative percentage variance of species–environment relation = 51.6 and 79.5%, for the first two axes respectively. Sum of all unconstrained eigenvalues (after fitting covariables) = 0.871, sum of all canonical eigenvalues = 0.250. Monte Carlo test, $P < 0.005$ for both axes

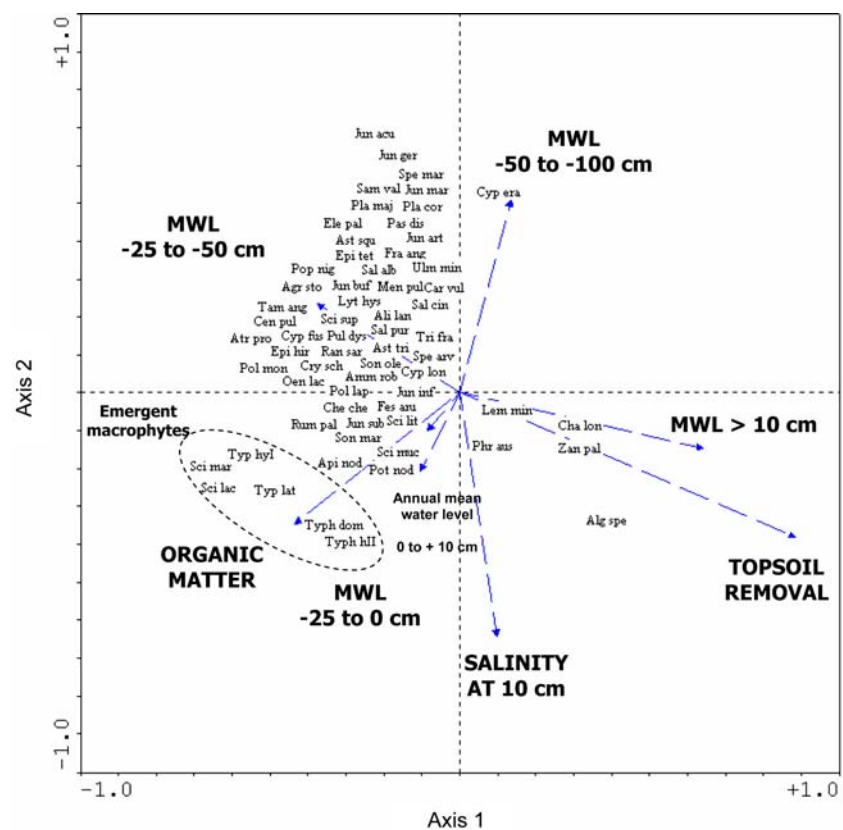


Fig. 6 Principal components analysis (PCA) of main study parcels (excluding topsoil-removed parcels). Eigenvalues = 0.434 and 0.161; cumulative percentage variance of species data = 43.4 and 59.5%, for the first two axes respectively. Sum of all unconstrained eigenvalues = 1.000

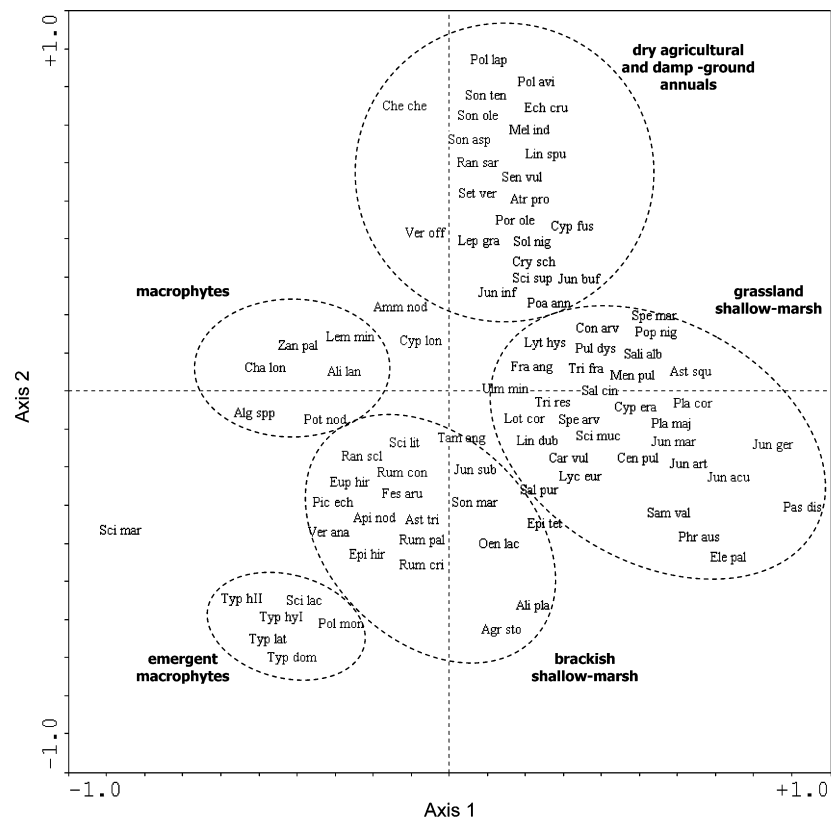


Table 1 Multiple linear regression models (stepwise procedure) for the two PCA axes of Fig. 6

Regression model	R ²	P
Axis 1 = - 0.989 - 0.00285 Summer MWL - 1.23 OM May at 30 cm - 1.34 Salinity at 10 cm in May	0.380	0.005
Axis 2 = 0.279 - 0.00286 Autumn MWL - 0.704 Salinity at 10 cm in August - 0.134 Time	0.390	0.004

R² is the adjusted determination coefficient

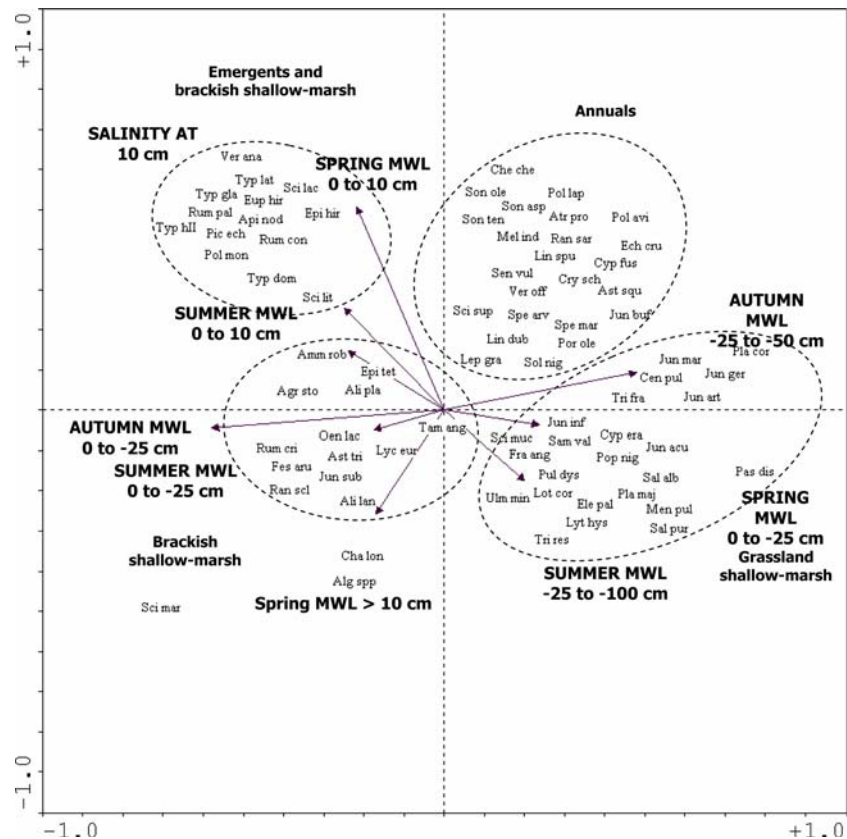
Discussion

The influence of water level on the plant communities

The principal environmental factor influencing vegetation composition in the developing Mediterranean wetland was water regime. More detailed analyses showed that summer and autumn irrigation were key water regime factors. This is not surprising given the Mediterranean climate and annual evapotranspiration deficit exceeding 600 mm.

The annual macrophytes *Zannichellia palustris*, *Chara* spp. and *Lemna minor* were associated with the highest water levels: annual MWL over 0 cm (preferably over 10 cm) and seasonal MWL over 10 cm. Macrophytes were abundant in the canals at the start of succession but decreased with time and had largely disappeared after 2 years of continuous flooding. Water in the canals was usually turbid from continued visitation by waterbirds. Also, the eutrophic water often suffered excessive phytoplankton growth, which probably decreased the light necessary for macrophyte germination and survival

Fig. 7 Partial redundancy analysis biplot with years as covariates and seasonal mean water level (MWL) classes (excluding topsoil-removed parcels). Other variables were topsoil removal and salinity at 10 cm in May (log-transformed). Eigenvalues = 0.314 and 0.096; species–environment correlations = 0.906 and 0.906; and cumulative percentage variance of species–environment relation = 50.9 and 66.5%, for the first two axes respectively. Sum of all unconstrained eigenvalues (after fitting covariables) = 0.764, sum of all canonical eigenvalues = 0.617. Monte Carlo test $P < 0.005$ for both axes



(Ribas-de-Pouplana et al. 1986; Consorci de la Costa Brava 1998). Organic matter accumulation causes sediments to become anoxic and may further reduce macrophyte production through toxic ferrous iron or sulphide production (Van Wijck et al. 1992; Van Wijck and De Groot 1993).

The emergent macrophytes *Typha latifolia*, *T. dominguensis*, *Typha* hybrids and *Scirpus lacustris* also had a high annual MWL of 0–10 cm, particularly requiring summer/autumn MWL from 0 to 10 cm i.e. continuous shallow irrigation ensuring a permanently waterlogged soil. Autumn irrigation was apparently very important; most rhizome production occurs in late autumn and rapid spring growth is based on these stored resources (Grace and Wetzel 1981). Comparable water levels are reported from the literature (e.g. *T. dominguensis* formed dense, impenetrable stands in 10–20 cm water, Grace and Wetzel 1982; McCoy and Rodríguez 1994). Changes in water level management after July 1997 caused rapid die-off of the emergents.

The time period of this study was not sufficient to assess in detail *Phragmites australis*, which was slow to establish (1.4% total cover after 4 years) but was expanding on all parcels after 4 years of abandonment from agriculture. Havens et al. (1997) found *P. australis* dominance increased sharply after the fifth year in constructed wetlands in the US.

The interactive influences of water level and salinity

Distribution of the annual macrophytes and the emergent vegetation at the study site was most likely influenced by the direct effects of water levels rather than by soil salinity (ranging from 0.57 to 4.1 mS/cm at the site). For natural wetland systems with freshwater inputs over saline sediment initial descriptions that salinity (to 15 mS/cm) determined vegetation pattern only in the broadest sense (Kadlec 1982) have been refined and soil conductivities over 10 mS/cm favour *Scirpus*

Table 2 Summary of the main plant assemblages and their relationship with environmental variables identified by multivariate analyses

Group	Typical species	Water levels	Soil
Annual and perennial macrophytes	<i>Zannichellia palustris</i> , <i>Chara vulgaris</i> var. <i>longibracteata</i> , <i>Lemna minor</i> , <i>Potamogeton nodosus</i>	Annual MWL > 0 cm or preferably > 10 cm (i.e. permanent standing water) and the deepest water levels (> 10 cm) during spring, summer and autumn	Abundance of annual macrophytes decreased with time. Associated with the first stages of succession and favoured by factors bringing system back to start point of succession (e.g. topsoil removal). Salinity at the levels found in the study was not limiting for <i>Typha</i> spp.
Emergent macrophytes	<i>Typha domingensis</i> , <i>T. latifolia</i> , <i>T. x glauca</i> , <i>Scirpus lacustris</i>	High annual MWL (0–10 cm) not as deep as the macrophytes, but require shallow irrigation in summer and autumn (preferably from 0 to 10 cm) to maintain a waterlogged soil	Positive effects of OM at 30 cm; positive effects of salinity
Shallow brackish marsh	<i>Polygonum monspeliensis</i> , <i>Agrostis stolonifera</i> , <i>Oenanthe lachenalii</i> , <i>Festuca arundinacea</i> , <i>Sonchus maritimus</i> , <i>Rumex palustris</i> , <i>Rumex crispus</i> , <i>Aster tripolium</i> , <i>Alisma plantago-aquatica</i> , <i>Euphorbia hirsuta</i> , <i>Epilobium tetragonum</i> , <i>Epilobium hirsutum</i> , <i>Juncus subulatus</i> , <i>Tamarix anglica</i>	Annual MWL – 25 to – 50 cm; positive effects of summer and autumn irrigation; episodes of water levels near the surface from 0 to – 25 cm; some species related to direct effects of these water levels, others to increased salinity	Negative effects of OM at 30 cm; negative effects of salinity
Grassland	<i>Paspalum distichum</i> , <i>Juncus acutus</i> , <i>J. gerardi</i> , <i>J. articulatus</i> , <i>Plantago major</i> , <i>Centaureum pulchellum</i> , <i>Eleocharis palustris</i> , <i>Samolus valerandi</i> , <i>Trifolium fragiferum</i> , <i>Salix alba</i> , <i>Salix cinerea</i> , <i>Carex vulpina</i> , <i>Aster squamatus</i> , <i>Mentha pulegium</i>	Annual MWL – 25 to – 50 cm; negative effects of summer and autumn irrigation; water levels below – 25 cm, which represents a salinity refuge; shallow flooding in spring (0 to – 25 m)	Negative effects of salinity; need exposed soil surface
Agricultural pioneers	<i>Polygonum aviculare</i> , <i>Linaria spuria</i> , <i>Sonchus oleraceus</i> , <i>S. tenerrimus</i> , <i>Melilotus indica</i> , <i>Verbena officinalis</i> , <i>Convolvulus arvensis</i> , <i>Solanum nigrum</i> , <i>Lepidium graminifolium</i>	Dry soil surface in summer	Negative effects of salinity; need exposed soil surface
Damp ground pioneers and weeds of irrigated fields and rice-fields	<i>Echinochloa crus-galli</i> , <i>Polygonum lapathifolium</i> , <i>Juncus bufonius</i> , <i>Lythrum hyssopifolia</i> , <i>Ammania robusta</i> , <i>Scirpus supinus</i> , <i>Cyperus difformis</i> , <i>Crypsis schoeniodes</i> , <i>Chenopodium chenopodioides</i>	Damp or irrigated soil surface in summer	Need exposed soil surface

MWL = mean water level, OM = organic matter concentration

maritimus or *S. olneyi* over *Typha* spp. (Bolen 1964; Kadlec and Smith 1989). Wetland species of Saskatchewan grassland were affected strongly by water regime and less by salinity (Walker and Coupland 1970, 1968) and a combination of factors (life history features, water level regimes and salinity) explained the responses of prairie marsh emergent macrophytes (Shay and Shay 1986).

Soil salinity was increased by summer and autumn irrigation. Soils in the area have a tendency to salinity caused by an historical connection with the sea and a partially saline water table (Bach 1990). Although flooding with freshwater pushes salts down into the sediments, summer and autumn irrigation increases evaporation which draws salts in the sediment or interstitial water to the surface by capillary action (Kadlec 1982; Kadlec and Smith 1989). Accumulation of salts at the surface is more pronounced with episodes of flooding and partial drying, which occurred in the summer flooded parcels when water supply was not sufficient to allow pumping. At the study site, the shallow water column would amplify this effect.

However, water levels indirectly influenced distribution of the shallow-marsh species by causing increased salinity. Separation of the shallow-marsh group into two assemblages is correlated with increased soil salinity and subsoil organic matter caused by summer and autumn irrigation. The grassland assemblage (including *Juncus articulatus*, *Plantago major*, *Trifolium fragiferum*, *Carex vulpina* and *Paspalum distichum*) was characterised with annual MWL of –25 to –50 cm, winter MWL of 0 to 10 cm, and shallow flooding in spring (0 to –25 cm) but the key requirement was summer/autumn water levels below –25 cm, where salinity is lower. *P. distichum*, an introduced grass from Asia, was the dominant perennial of the shallow-marsh and the second most abundant species at the site during the study. In its native freshwater Indian wetlands it is reported from a wide MWL range (1–89 cm) (Middleton et al. 1991) but is sensitive to salinity; Mesléard et al. (1993) reported a reduction in mean yield at salinities of 3.1 mS/cm and absence at salinities of 6 mS/cm. It is likely that the grassland assemblage water regime meets the hydrological needs of *P. distichum* while avoiding salinity and represent a salinity ‘refuge’.

Distribution of this assemblage was therefore constrained by relatively low levels of salinity. The key difference for the brackish assemblage were episodes of water levels near the surface (MWL of 0 to –25 cm) in summer and autumn, which led to increased salinity. This subgroup includes typical species of brackish salt-marshes, such as *Polypogon monspeliensis*, *Juncus subulatus* or *Oenanthe lachenalii* or with some tolerance of salinity (*Euphorbia hirsuta*, *Epilobium hirsutum*, *Rumex palustris*) (Bolòs and Vigo 1984). *Tamarix anglica* was common on these parcels and abundance would be expected to increase over longer time periods. Species from this group also form the vegetation on parcels salinised by previous episodes of irrigation.

The most abundant species at the site, *Scirpus maritimus*, showed a wide ecological amplitude. *Scirpus maritimus* distribution was not limited by soil salinity over the range found (0.57–4.1 mS/cm). Its natural habitat is on the edge of brackish or saline pools with large variations in water chemistry, particularly conductivity (Liefvers and Shay 1982; Kadlec and Smith 1989).

Succession

Time since abandonment was a further key source of variation in the full data set. Annuals were differentiated by time only from perennials (not by water level requirements). A key requirement for annuals are bare surfaces for germination. The “dry” annual group are common agricultural weeds such as *Sonchus tenerrimus* or *Lepidium graminifolium*, while many “damp” annuals are common weeds of irrigated crops in the region (e.g. *Echinochloa crus-galli*, *Polygonum lapathifolium*, *Lythrum hyssopifolia*). Humid bare ground specialists such as *Scirpus supinus* and *Crypsis schoeniodes* were also present in this group. Abundance of all these species decreased over the 4-year study period, as bare ground habitat disappeared.

Management implications and spatial heterogeneity of vegetation

The preceding conclusions have some important implications for management. Rehabilitation of

the abandoned ricefields in the Natural Park is largely intended to create marshes attractive for birds such as black-winged stilt (*Himantopus himantopus*) or little grebe (*Tachybaptus ruficollis*) (Sargatal 1995). Periodical drawdown in the canals would oxidise toxic sediments (Kadlec 1962; Van Wijck et al. 1992) and help maintain macrophyte populations, an important waterfowl foodsource (Kadlec and Smith 1989). The macrophytes showed a clear preference for soils with little organic matter, found early in the study period, and where topsoil was removed. *Z. palustris*, *Ranunculus baudotii* and *Chara* spp. are a common feature of Mediterranean temporary marshes dry for at least one month a year (Grillas et al. 1991). Waterbirds favour a heterogeneous habitat dominated by *Scirpus maritimus* and non-dense *Typha* spp. (Comin et al. 1997) and *H. Himantopus* choose shallowly flooded plots with sparse *S. maritimus* to nest (Sargatal 1995). *Scirpus maritimus* is abundant in the first years but decreases over time. Sediment conductivity at the site is not high enough to allow *Typha* spp. control through salinity, but this could be achieved through drawdown (water levels below –10 cm) after flooding at 0–10 cm through 2 years causing *Typha* spp. dieoff and favouring *S. maritimus*. *P. distichum* dominance can be controlled, and diversity increased, using episodes of drawdown where water tables are maintained within several centimeters of the soil surface (causing soil salts to accumulate in the soil layer).

Spatial vegetation heterogeneity in the developing abandoned ricefield vegetation is influenced by the managed water regime, and to a lesser extent salinity. In natural wetlands, topography would influence spatial variation in water regime and thereby spatial vegetation patterns. Vegetation heterogeneity in the developing abandoned ricefields corresponds to a pattern of intra-parcel homogeneity and inter-parcel heterogeneity, a reflection of the engineered past. Maintenance of spatial vegetation heterogeneity and the associated benefits for wildlife conservation is therefore dependent on continued water regime management.

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Appendix 1 Mean Species Cover Values (1995–1998) with acronyms used for ordination plots

Plant Assemblage	Acronym	Mean cover
Annual and perennial macrophytes		
<i>Chara vulgaris</i> var. <i>longibractea</i>	<i>Cha lon</i>	2.07
Algae	<i>Alg spp.</i>	1.37
<i>Zannichellia palustris</i>	<i>Zan pal</i>	1.17
<i>Lemna minor</i>	<i>Lem min</i>	<0.01
<i>Potamogeton nodosus</i>	<i>Pot nod</i>	<0.01
Emergent macrophytes		
<i>Typha latifolia</i>	<i>Typ lat</i>	3.23
<i>Typha dominguensis</i>	<i>Typ dom</i>	2.65
<i>Scirpus lacustris</i>	<i>Sci lac</i>	0.70
<i>Typha glauca</i>	<i>Typ gla</i>	0.46
<i>Typha hybrid II</i>	<i>Typ hII</i>	0.27
Shallow brackish marsh		
<i>Agrostis stolonifera</i>	<i>Agr sto</i>	1.76
<i>Polygonum monspeliensis</i>	<i>Pol mon</i>	1.73
<i>Juncus subulatus</i>	<i>Jun sub</i>	0.20
<i>Alisma plantago-aquatica</i>	<i>Ali pla</i>	0.16
<i>Veronica anagallis-aquatica</i>	<i>Ver ana</i>	0.09
<i>Tamarix anglica</i>	<i>Tam ang</i>	0.06
<i>Epilobium hirsutum</i>	<i>Epi hir</i>	0.05
<i>Epilobium tetragonum</i>	<i>Epi tet</i>	0.04
<i>Apium nodiflorum</i>	<i>Api nod</i>	0.03
<i>Aster tripolium</i>	<i>Ast tri</i>	0.03
<i>Rumex crispus</i>	<i>Rum cri</i>	0.02
<i>Oenanthe lachenalii</i>	<i>Oen lac</i>	0.02
<i>Festuca arundinacea</i>	<i>Fes aru</i>	<0.01
<i>Rumex palustris</i>	<i>Rum pal</i>	<0.01
<i>Sonchus maritimus</i>	<i>Son mar</i>	<0.01
<i>Euphorbia hirsuta</i>	<i>Eup hir</i>	<0.01
<i>Scirpus littoralis</i>	<i>Sci lit</i>	<0.01
<i>Lycopus europeus</i>	<i>Lyc eur</i>	<0.01
<i>Rumex conglomeratus</i>	<i>Rum con</i>	<0.01
Grassland shallow-marsh		
<i>Paspalum distichum</i>	<i>Pas dis</i>	12.66
<i>Aster squamatus</i>	<i>Ast squ</i>	1.73
<i>Plantago major</i>	<i>Pla maj</i>	0.50
<i>Juncus acutus</i>	<i>Jun acu</i>	0.95
<i>Juncus gerardi</i>	<i>Jun ger</i>	0.15
<i>Juncus articulatus</i>	<i>Jun art</i>	0.09
<i>Eleocharis palustris</i>	<i>Ele pal</i>	0.60
<i>Mentha pulegium</i>	<i>Men pul</i>	0.05
<i>Juncus maritimus</i>	<i>Jun mar</i>	0.03
<i>Plantago coronopus</i>	<i>Pla cor</i>	0.02
<i>Picris echiodes</i>	<i>Pic ech</i>	0.02

Appendix 1 continued

Plant Assemblage	Acronym	Mean cover
<i>Samolus valerandi</i>	<i>Sam val</i>	0.02
<i>Populus nigra</i>	<i>Pop nig</i>	0.01
<i>Salix alba</i>	<i>Sal alb</i>	<0.01
<i>Fraxinus angustifolia</i>	<i>Fra ang</i>	<0.01
<i>Lotus corniculatus</i>	<i>Lot cor</i>	<0.01
<i>Ranunculus sceleratus</i>	<i>Ran sce</i>	<0.01
<i>Trifolium fragiferum</i>	<i>Tri fra</i>	<0.01
<i>Scirpus mucronatus</i>	<i>Sci muc</i>	<0.01
<i>Trifolium resupinatum</i>	<i>Tri res</i>	<0.01
<i>Pulicaria dysenterica</i>	<i>Pul dys</i>	<0.01
<i>Centaurium pulchellum</i>	<i>Cen pul</i>	<0.01
<i>Oryzopsis miliacea</i>	<i>Ory mil</i>	<0.01
<i>Cyperus eragrostis</i>	<i>Cyp era</i>	<0.01
<i>Salix purpurea</i>	<i>Sal pur</i>	<0.01
<i>Carex vulpina</i> ssp. <i>nemorosa</i>	<i>Car vul</i>	<0.01
<i>Salix cinerea</i> ssp. <i>oleifolia</i>	<i>Sal cin</i>	<0.01
<i>Ulmus minor</i>	<i>Ulm min</i>	<0.01
Agricultural pioneers		
<i>Atriplex prostrata</i>	<i>Atr pro</i>	0.44
<i>Sonchus oleraceus</i>	<i>Son ole</i>	0.05
<i>Sonchus tenerrimus</i>	<i>Son ten</i>	0.05
<i>Sonchus asper</i>	<i>Son asp</i>	0.04
<i>Cyperus fuscus</i>	<i>Cyp fus</i>	0.13
<i>Ranunculus sardous</i>	<i>Ran sar</i>	0.01
<i>Polygonum aviculare</i>	<i>Pol avi</i>	0.02
<i>Solanum nigrum</i>	<i>Sol nig</i>	<0.01
<i>Lepidium graminifolium</i>	<i>Lep gra</i>	<0.01
<i>Setaria verticillata</i>	<i>Set ver</i>	<0.01
<i>Poa annua</i>	<i>Poa ann</i>	<0.01
<i>Linaria spuria</i>	<i>Lin spu</i>	<0.01
<i>Melilotus indica</i>	<i>Mel ind</i>	<0.01
<i>Senecio vulgaris</i>	<i>Sen vul</i>	<0.01
Damp ground pioneers and weeds of irrigated fields and rice-fields		
<i>Echinochloa crus-galli</i>	<i>Ech cru</i>	0.55
<i>Chenopodium chenopodioides</i>	<i>Che che</i>	0.51
<i>Polygonum lapathifolium</i>	<i>Pol lap</i>	0.41
<i>Lythrum hyssopifolia</i>	<i>Lyt hys</i>	0.04
<i>Juncus bufonius</i>	<i>Jun buf</i>	0.02
<i>Scirpus supinus</i>	<i>Sci sup</i>	0.02
<i>Crypsis schoenoiodes</i>	<i>Cry sch</i>	0.01
<i>Verbena officinalis</i>	<i>Ver off</i>	<0.01
<i>Lythrum salicaria</i>	<i>Lyt sal</i>	<0.01
<i>Spergula arvensis</i>	<i>Spe arv</i>	<0.01
<i>Portulaca oleracea</i>	<i>Por ole</i>	<0.01
Non-specific		
<i>Scirpus maritimus</i>	<i>Sci mar</i>	29.90
<i>Phragmites australis</i>	<i>Phr aus</i>	0.45
<i>Ammania robusta</i>	<i>Amm rob</i>	0.30
<i>Lindernia dubia</i>	<i>Lin dub</i>	0.05
<i>Convolvulus arvensis</i>	<i>Con arv</i>	0.01
<i>Spergularia maritima</i>	<i>Spe mar</i>	<0.01
<i>Juncus inflexus</i>	<i>Jun inf</i>	<0.01
<i>Cyperus longus</i>	<i>Cyp lon</i>	<0.01
<i>Alisma lanceolatum</i>	<i>Ali lan</i>	<0.01

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