

## FLORISTIC COMPOSITION OF ANTHROPOGENIC SEASONAL WETLANDS IN THE COASTAL MOUNTAIN RANGE OF CAUTIN, CHILE

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### ABSTRACT

**Keywords:** Ephemeral wetland vegetation, vernal pools, aquatic plants, life forms.

Secondary anthropogenic temporary wetlands are formed in seasonally flooded landscape depressions in the mountainous region of Tromen (Region Araucanía, Chile). We sampled 80 plots of 25 m<sup>2</sup> distributed between 10 seasonal wetlands, estimating the cover of plant species in each plot. We analysed the taxonomic composition, status and life-forms of the flora and compared the species composition of the wetlands through classification (hierarchical clustering) and ordination (nMDS) analyses. The floristic composition of the wetlands was very heterogeneous. Their species richness was not correlated or other their area size or their community composition. The high importance of introduced plant species and the low number of ephemeral wetland specialists in the studied flora (only 9 specialists of 87 species) confirmed the secondary character of the studied wetlands. The effects of disturbance on the seasonal wetland flora are also discussed.

### RESUMEN

**Composición florística de lagunas temporales antropogénicas en las montañas costeras de Cautín, Chile**

**Palabras clave:** vegetación de lagunas temporales, humedales, plantas acuáticas, formas de vida.

Lagunas efímeras se han formado secundariamente en depresiones inundadas estacionalmente en la región montañosa de Tromen (Región de la Araucanía, Chile). En este trabajo se levantaron 80 censos vegetales en parcelas de 25 m<sup>2</sup> distribuidas en 10 lagunas temporales, estimando visualmente la cobertura de las especies en cada parcela. Se analizó la composición taxonómica, origen y formas de vida de las especies vegetales y se comparó la composición florística de las lagunas a través de análisis de clasificación (clusters jerárquicos) y de ordenación (nMDS). La composición florística de los humedales resultó ser muy heterogénea, mientras que su riqueza en especies no se correlaciona con su superficie ni con la cantidad de comunidades vegetales presentes en cada uno de ellos. La alta importancia de las especies introducidas y la baja participación de especialistas de lagunas efímeras (sólo 9 especies de 87) en la cubierta vegetal confirman el carácter secundario de los humedales estudiados. También se discuten los efectos de la alteración en la flora de lagunas temporales.

## INTRODUCTION

The region of Temuco was originally covered with native forests. In the uplands these forests were partially deciduous with some sclerophyllous elements, while in the lower areas and near the rivers they were dominated by evergreen elements (Ramírez *et al.* 1989). This original forest vegetation was destroyed during the colonization of this region (Ramírez *et al.* 1988, Otero 2006).

Originally swampy myrtaceous forest grew in the landscape depressions that were seasonally flooded (Ramírez *et al.* 1983). After the deforestation, those depressions became seasonal wetlands: wetlands that are flooded in winter by seasonal rainfall and small streams, but are completely dry during the summer (Deil 2005). The dry periods, over the last few years, have become extended, due to low rainfall and the infilling of the wetlands with sediment.

In Chile, there is little knowledge concerning the flora and ecology of seasonal wetlands. Published studies are restricted to first observations by Oberdorfer (1960), a preliminary sur-

vey of the flora and the distribution of vernal pools by Bliss *et al.* (1998) and some regional investigations in Southern Chile (Ramírez *et al.* 1994, San Martín *et al.* 1998, Alvarez 2008). Throughout the world, seasonal wetlands are important ecosystems due to the presence of many palaeo and neo endemics (both plants and animals) and because of their vulnerability (Grillas *et al.* 2004, Deil 2005).

The aim of this research was to answer the following questions:

1) How important is wetland size in the determination of its species richness?

2) Do the floristic similarities between wetlands depend on their isolation?

3) Are there correlations between diversity and disturbance as estimated through biological indicators such as life-forms and the species status?

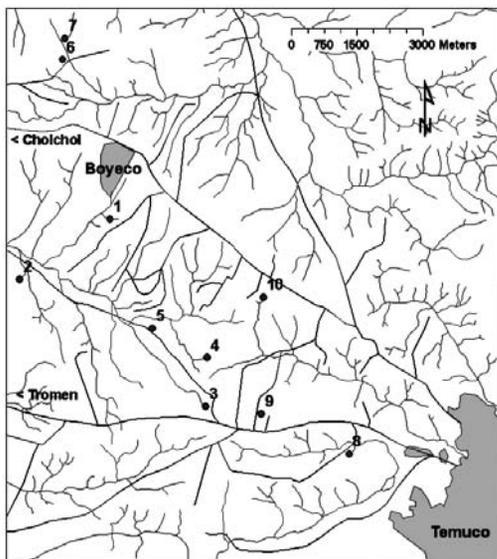
We expect a positive correlation between the area of the wetlands and their species richness following the predictions of the island biogeography hypothesis (MacArthur y Wilson 1967). Seasonal wetlands are normally fragmented ecosystems and the plant species that grow in them have adaptations to restrict their dispersal (Zedler 1990, Alvarez 2008). Therefore, a negative correlation between the similarity and the distance between wetlands is expected. Finally a correlation between the disturbance level and the species richness is expected. In addition, the importance of introduced species for the species richness of the wetlands will be discussed.

## MATERIAL AND METHODS

### Study site

The study site lies in the mountainous region of Tromen, to the west of Temuco (Figure 1). Most of the studied wetlands are located within the indigenous reserves of the Mapuche, who live in a precarious socio-economic situation and practice extensive, traditional agriculture. Because of the land-use history: extensive deforestation followed by intensive grain cultivation at the end of the 19<sup>th</sup> century (Berninger 1929, Otero 2006), the soils have been seriously degraded by erosion.

All of the wetlands but one are flooded seasonally.



**Figure 1.** Location of the studied wetlands near Temuco (Araucanía, Chile). Grey lines: small streams. Black lines: Ways and Streets.

**Figura 1.** Ubicación de las lagunas estudiadas en las cercanías de Temuco (Araucanía, Chile). Líneas grises: arroyos y desaguaderos. Líneas negras: calles y caminos.

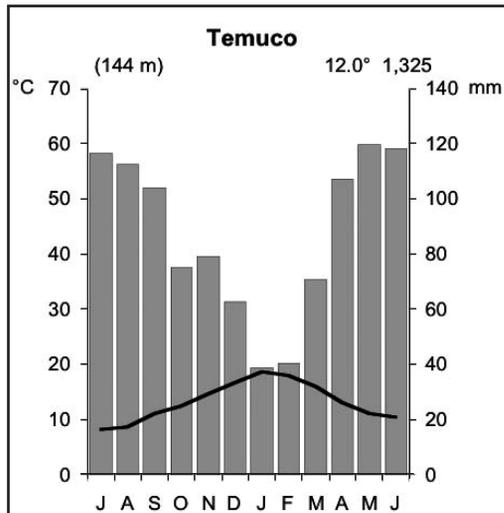


Figure 2. Climate diagram of Temuco. After Hajek y di Castri (1975).

Figura 2. Climodiagrama de Temuco. Según Hajek y di Castri (1975).

nally during the winter and subject to drought during the summer. Wetland number 8 on the farm 'Fundo Carmen Chico', belongs to descendants of German colonists, and is the only one with permanent water due to a dyke and the shading of surrounding trees. However, in the autumn 1999 after this study was concluded, this wetland was drained for construction work.

The soil in this area is classified as "red-loam type" and belongs to the Metrenco serie (Be-

soain 1985). It is considered to be a very heavy soil and difficult to cultivate. Opportunities for cultivation are restricted to a few weeks in the year, because of the drought in summer and the excess of soil moisture in winter. Soil erosion is widespread and constantly fills the bottom of landscape depressions with sediment.

According to the classification of Rivas-Martínez (1993), the climate belongs to the humid mesotemperate type (Amigo y Ramírez 1998). The annual rainfall reaches about 1,400 mm and the mean temperature is 12°C (di Castri y Hajek 1976). Rainfall is abundant in winter, and in summer there is a dry period of between one and three months (Figure 2). The natural vegetation is a subtropical semideciduous forest type (Schmithüsen 1956, Ramírez *et al.* 1998).

#### Data sampling

During the spring and summer of 1997 and 1998, 80 vegetation samples were taken from ten wetlands. The samples, 25 m<sup>2</sup> in size, were divided into stands of different communities (Table 1), including aquatic, limnic and terrestrial phases (Pott y Remy 2000). For each sample, the cover of the plant species was estimated (Dierschke 1994). A detailed description of the communities was presented by San Martín *et al.* (1998) and Hauenstein *et al.* (2002).

Nomenclature of the specific taxa was based

Table 1. List of the plant communities with their abbreviations and important plant species.

Cuadro 1. Lista de las comunidades vegetales con sus abreviaciones y especies importantes.

Community name	Abbr.	Important species
Anthoxanthum utriculatum-community	Au	<i>Anthoxanthum utriculatum</i> , <i>Leontodon taraxacoides</i> , <i>Juncus procerus</i> , <i>Mentha pulegium</i>
Eleocharis-Lythrum-community	EL	<i>Lythrum portula</i> , <i>Eleocharis pachycarpa</i> , <i>Glinus radiatus</i>
Eleocharietum macrostachyae	Em	<i>Eleocharis macrostachya</i> , <i>M. pulegium</i> , <i>Gratiola peruviana</i>
Eleocharietum pachycarpae	Ep	<i>E. pachycarpa</i> , <i>M. pulegium</i> , <i>G. peruviana</i>
Glycerietum multiflorae	GM	<i>Glyceria multiflora</i> , <i>Sagittaria montevidense</i> , <i>Ludwigia peploides</i>
Gnaphalio-Polygonetum	GP	<i>Gnaphalium cymatoides</i> , <i>Polygonum hydropiperoides</i> , <i>M. pulegium</i>
Junco-Caricetum	JC	<i>Carex riparia</i> , <i>Agrostis capillaris</i> , <i>J. procerus</i>
Juncetum proceri	Jp	<i>J. procerus</i> , <i>A. capillaris</i> , <i>M. pulegium</i> , <i>Lotus uliginosus</i>
Ludwigia-Sagittaria-community	LS	<i>S. montevidense</i> , <i>L. peploides</i> , <i>Callitriche terrestris</i>
Mentho-Agrostietum	MA	<i>M. pulegium</i> , <i>P. hydropiperoides</i> , <i>L. taraxacoides</i>
Phyla nodiflora-community	Pn	<i>Phyla nodiflora</i> , <i>E. macrostachya</i> , <i>Setaria parvifolia</i>
Potamogeton pusillus-community	Pp	<i>Potamogeton pusillus</i>

on Marticorena y Quezada (1985), and the family classification on Woodland (1991). Specialist literature was used to determine the classification of the rushes (Kirschner 2002) and the European plant species (Tutin *et al.* 1996). The author abbreviations in the appendix follow the proposal of Brummitt y Powell (1992).

### Data analysis

Constancy percent and relative cover of each species was calculated. The importance value was calculated as the mean value of these indices (Ramírez *et al.* 1997). Spectra according to the status and the life-forms of the sampled species were drawn. The information about the status of the species was obtained from Marticorena y Quezada (1985) and Matthei (1995). The life-forms were determined according to Raunkjær's classification using the key of Ellenberg y Mueller-Dombois (1966). A further ecological classification of the plant species follows Sculthorpe (1967) and Zedler (1990). The floristic composition of the wetlands was assessed at the species, genus and family level using taxonomic diversity profiles (Feoli y Scimone 1984).

Single and multiple linear regressions were carried out to assess models of the wetland species richness versus wetland area and the number of present communities. The data were all Log transformed (log10). The phytosociological reference for the communities was that described by San Martín *et al.* (1998) and Hauenstein *et al.* (2002). The correlation between beta diversity (pair wise comparison of the floristic composition using the Jaccard index; Jaccard 1912) and the distance between wetlands was also determined.

The floristic composition of seasonal wetlands was classified by hierarchical clustering with the complete linkage algorithm and the Jaccard index as the similarity measure (Leyer y Wesche 2007).

For an ordination analysis, a matrix with the importance value of each species in each wetland was arranged. Then a distance matrix was calculated using the Bray-Curtis-index (Bray y Curtis 1957). Finally a non-metric multidimensional scaling (nMDS) with two dimensions was carried out (Kruskal 1964). To compare the ordination axes with the proportion of therophytes, hemicryptophytes and introduced spe-

cies post-hoc, Poison correlations were carried out (Leyer y Wesche 2007). These proportions were used as disturbance indicators, based on the dominance of introduced species in secondary grassland communities of Southern Chile, the pioneer character of the therophytes (most of them also adventives) and the adaptation of hemicryptophytes to grazing and trampling (Hauenstein *et al.* 1988, Ramírez *et al.* 1991). The community composition of the wetlands was also compared with the ordination diagram, but using the Spearman rank-correlation. Both community composition and proportion of disturbance indicators were included in the ordination plot through a linear regression with the nMDS-dimensions (Leyer y Wesche 2007).

All above-mentioned analyses were performed using the software R version 2.8 (R Development Core Team 2005) including the packages vegan, cluster and simba.

## RESULTS

### Taxonomic diversity of flora

In total 87 plant species belonging to 71 genera and 35 families were sampled (Table 2). The class with the highest number of species was Magnoliopsida (dicotyledons) with 55 species (about 63 % of the total number), 32 species (37 %) belonged to the class Liliopsida (monocotyledons). A total of 52.9 % of the total plant cover were monocotyledons. No ferns were found in these wetlands.

The families with the greatest representation were Poaceae with 14 species in 14 genera and Asteraceae with 12 species in 11 genera, 16 and 14 % of the total species number, respectively. The most common families of the Magnoliopsida after Asteraceae were Polygonaceae (6

**Table 2. Number of plant taxa present in the seasonal wetlands near Temuco.**

**Cuadro 2. Número de taxa vegetales presentes en lagunas temporales cerca de Temuco**

Class	Families	Genera	Species (%)
Magnoliopsida	28	47	55 (63.22)
Liliopsida	7	24	32 (36.78)
Total	35	71	87 (100.00)

**Table 3. Frequency in the vegetation samples and in the wetlands, importance value and status of the most common species in the seasonal wetlands near Temuco.****Cuadro 3. Frecuencia en los censos y en las lagunas, valor de importancia y origen de las especies más comunes en las lagunas temporales cerca de Temuco.**

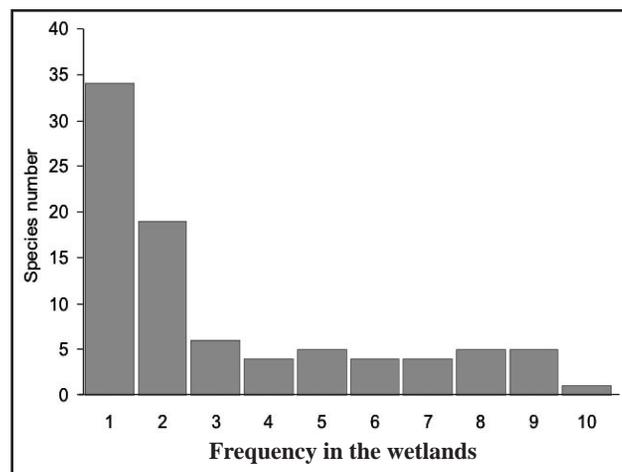
Species	Frequency in samples	Total cover	Importance value	Frequency in wetlands	status
<i>Mentha pulegium</i>	54	1,077	40.48	9	introduced
<i>Leontodon taraxacoides</i>	39	365	26.66	8	introduced
<i>Eleocharis pachycarpa</i>	31	928	25.18	9	native
<i>Polygonum hydropiperoides</i>	36	247	24.04	10	introduced
<i>Juncus procerus</i>	26	895	21.84	9	native
<i>Agrostis capillaris</i>	29	522	21.39	8	introduced
<i>Phyla nodiflora</i>	25	440	18.38	9	introduced
<i>Lotus uliginosus</i>	26	224	17.65	8	introduced
<i>Gratiola peruviana</i>	27	119	17.62	9	native
<i>Cyperus reflexus</i>	25	25	15.78	8	native
<i>Eleocharis macrostachya</i>	19	476	14.85	6	native
<i>Gnaphalium cymatoides</i>	20	301	14.38	7	native
<i>Centipeda elatinooides</i>	19	78	12.36	8	native
<i>Rumex conglomeratus</i>	18	18	11.36	7	introduced

species in 3 genera), Apiaceae (4 species in 3 genera), Scrophulariaceae (4 species in 4 genera) and Fabaceae (3 species in 2 genera). For the Liliopsida, the families Cyperaceae (7 species in 4 genera) and Juncaceae (6 species, all in the genus *Juncus*) followed the grasses in order of importance.

*Mentha pulegium*, an introduced chamaephyte, was the most important species in the vegetation samples (Table 3). This species grows in wet grasslands and colonizes the borders of the wetlands. A total of 14 plant species were pre-

sent in more than 10 samples, including 7 introduced species (*Agrostis capillaris*, *Leontodon taraxacoides*, *Lotus uliginosus*, *M. pulegium*, *Phyla nodiflora*, *Polygonum hydropiperoides* and *Rumex conglomeratus*) and 7 native species (*Centipeda elatinooides*, *Cyperus reflexus*, *Eleocharis macrostachya*, *Eleocharis pachycarpa*, *Gnaphalium cymatoides*, *Gratiola peruviana* and *Juncus procerus*), most of which were hemicryptophytes.

More than a 60 % of the species were found in only 1 or 2 wetlands (Figure 3). Only 1 spe-

**Figure 3. Frequency histogram of the species in the wetlands near Temuco.****Figura 3. Histograma de frecuencia de las especies en las lagunas de las cercanías de Temuco.**

**Table 4. Proportion of classes and status of the seasonal wetland flora near Temuco.****Cuadro 4. Proporción de clases y orígenes de la flora de lagunas temporales cerca de Temuco.**

Class	natives	introduced	Total
Magnoliopsida	25 (28.74)	30 (34.48)	55
Liliopsida	20 (22.99)	12 (13.79)	32
Total	45 (51.72)	42 (48.28)	87

Percentage in parentheses

cies (*Polygonum hydropiperoides*) was found in all 10 wetlands. Five species occurred in 9 wetlands: *Eleocharis pachycarpa*, *Gratiola peruviana*, *Juncus procerus*, *Mentha pulegium* and *Phyla nodiflora*, of those the last two species are introduced. *Agrostis capillaris*, *Centipeda elatinoides*, *Cyperus reflexus*, *Leontodon taraxacoides* and *Lotus uliginosus* were present in 8 wetlands, of those only *C. elatinoides* and *C. reflexus* are native. *Eryngium pseudojunceum*, *Glyceria multiflora*, *Gnaphalium cymatoides* and *Rumex conglomeratus*, were present in 7 wetlands, and all are natives except the last one. *Eleocharis macrostachya*, *Hypochaeris radicata*, *Juncus microcephalus* and *Spergularia rubra* were only found in 6 wetlands.

#### Life-forms and status of the species

From the sampled species, 45 (51.7 %) are native and 42 (48.3 %) are introduced (Table 4). With respect to the cover values, the native species account for 54.5 % of the total cover.

The most abundant life-form was the hemicryptophytic with 39 species, representing about 45 % of the total (Table 5, Figure 4). This life-form was abundant on the banks of

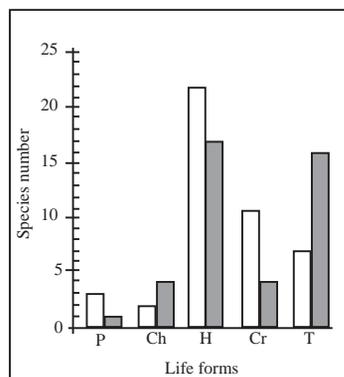
**Table 5. Proportion of life-forms in the seasonal wetland flora near Temuco.****Cuadro 5. Proporción de las formas de vida en la flora de lagunas temporales cercanas a Temuco.**

Life-forms	Species	Cover
phanerophytes P	4 (4.60)	13 (0.17)
chamaephytes Ch	6 (6.90)	1,238 (16.08)
hemicryptophytes H	39 (44.83)	4,890 (63.52)
cryptophytes Cr	15 (17.24)	1,078 (14.00)
therophytes T	23 (26.44)	479 (6.22)
Total	87	7,698

Percentage in parentheses

the wetlands and the higher surrounding areas. The second most important life-form were the therophytes (annual herbs), represented by 23 species (26.4 %). They colonize the innermost part of the wetlands. The cryptophytes (perennial herbs with underground survival organs) were represented by 15 species (17.2 %) and the other life-forms present include hydrophytes (aquatic plants), helophytes (swamp plants) and one geophyte (the bulb herb *Sisyrinchium graminifolium*). Both hydrophytes and helophytes grow along the shores and in the shallow water of the wetlands. Chamaephytes (perennial herbs and dwarf scrubs with shoot apices close to the soil surface) and phanerophytes (all other woody plants) were the most scarce life-forms with 6 and 4 species, respectively. Taking cover values into account, the proportion of hemicryptophytes was the greatest (63.5 %), followed by chamaephytes, cryptophytes, therophytes and phanerophytes, in decreasing order of importance (Table 5).

Separating the native species from the introduced species, about 70 % of the therophytes are introduced, whereas cryptophytes and hemicryptophytes are predominantly native species (Figure 4).

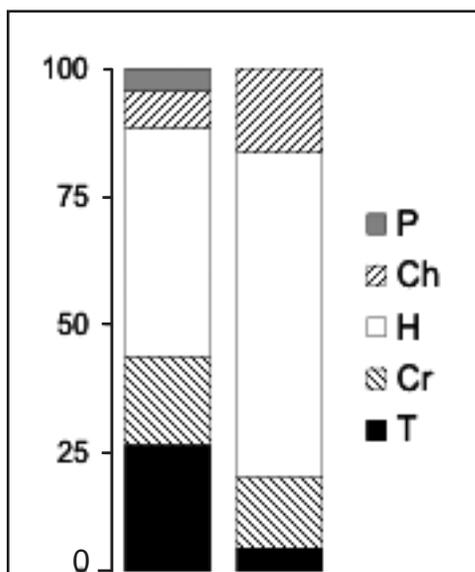


**Figure 4. Comparison between native (white bars) and adventive plants (grey bars) in the life-form spectrum of the wetlands near Temuco. Life-forms: phanerophyte (P), chamaephyte (Ch), hemicryptophyte (H), cryptophyte (Cr) and therophyte (T).**

**Figura 4. Comparación entre especies nativas (barras blancas) y adventivas (barras grises) en el aspecto biológico de las lagunas de las cercanías de Temuco. Formas de vida: fanerófito (P), caméfito (Ch), hemicriptófito (H), criptófito (Cr) y terófito (T).**

**Figure 5. Life-form spectra according to the species number (left) and the cover (right). Life-forms: phanerophyte (P), chamaephyte (Ch), hemicryptophyte (H), cryptophyte (Cr) and therophyte (T).**

**Figura 5. Espectro biológico de acuerdo al número de especies (izquierda) y a su cobertura (derecha). Formas de vida: fanerófita (P), caméfito (Ch), hemicriptófita (H), criptófita (Cr) y terófita (T).**



### Ecology of the sampled plant species

The biological spectrum (Figure 5) corresponds to the therophitic phytoclimate typical of the northeast region of Central Chile (San Martín y Ramírez 1986). In the studied wetlands this biological spectrum was more developed in the dry summer months (during the terrestrial phase sensu Pott y Remy 2000). In the wettest season (winter and spring) perennial life-forms of hemicryptophytes, hydrophytes and helophytes (cryptophytes) become dominant. The therophytes were only found in the terrestrial phase, whereas the hemicryptophytes and cryptophytes were found throughout the year. A similar seasonality was found in Southern Chilean grasslands by Ramírez (1984).

Comparing the species list of this work with those of Ramírez *et al.* (1983), 9 species of the native flora and 12 of the introduced flora have an affinity with the myrtaceous swamp forest,

which originally grew in these wetlands. On the other hand, typical ephemeral wetland species are not very important, taking as a reference the works of Ramírez *et al.* (1994), Bliss *et al.* (1998) and Álvarez (2008). About 49 % of the total sampled species (43 species) were terrestrial plants belonging to dry locations (Table 6). Swamp plants comprised 41 % (36 species) of all collected plants. Aquatic plants accounted for only 9 % (8 species) of the flora, of which 5 are submerged plants (*Myriophyllum aquaticum*, *Utricularia gibba*, *Limosella australis*, *Crassula peduncularis*, and *Potamogeton pusillus*) and 2 were floating leaved species (*Ludwigia peploides*, *Callitriche palustris* and *Callitriche autumnalis*). These water plants (almost the aerial parts) disappear in the dry seasons. Using cover values as a measure, helophytes accounted for 70 % of the vegetation and 50 % according to the total species number. This confirms the importance of the swamp flora along the wetland shores and the seasonality of these habitats, which represent amphibious ecosystems alternating very wet periods with very dry ones (Deil 2005, Chambers *et al.* 2008).

Of the 87 species that formed the flora of the studied wetlands, only 9 (10.34 %) were obligate ephemeral wetland plants (Zedler 1990). Eight were dicotyledons and one (*Juncus stipulatus*) was a monocotyledon, all of which were native species, the hemicryptophytes *Centipeda elatinoides*, *Eryngium humifusum*, *Eryngium pseudojunceum* and *Phyla nodiflora*, the therophytes *Glycyrrhiza radiatus*, *Gnaphalium cymatoides*, *Navarretia involucreta* and *Juncus stipulatus*, and the cryptophyte *Lythrum portula*. The majority of these are small and colonize the

**Table 6. Distribution of plant species according to their habitat.**

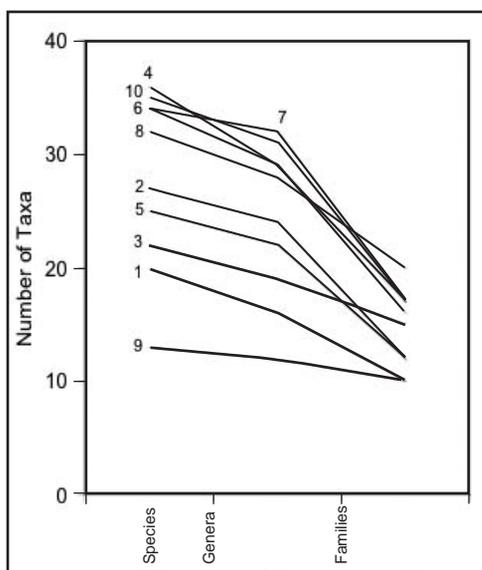
**Cuadro 6. Distribución de las especies vegetales de acuerdo a su hábitat.**

Habitat	Species	Cover
Dryland plants	43 (49.43)	2,186 (28.40)
Swamp plants	36 (41.38)	5,343 (69.41)
Aquatic plants	8 (9.20)	169 (2.19)
Total	87	7,698

Percentage in parentheses

**Table 7. Area, number of vegetation samples, communities and species in the studied wetlands.**  
**Cuadro 7. Área, número de censos, comunidades vegetales y especies en las lagunas estudiadas.**

Pool	Surface (ha)	Samples	Communities	Species	Percentage of the total
1	0.27	7	3	20	23.00
2	0.45	8	3	27	31.03
3	3.60	11	3	22	25.29
4	2.88	14	4	36	41.38
5	0.10	7	3	25	28.74
6	0.90	9	5	34	39.08
7	0.15	4	3	34	39.08
8	0.32	8	3	32	36.78
9	0.36	3	1	13	14.94
10	0.90	9	5	35	40.23



**Figure 6. Taxonomic diversity profile of the studied wetlands.**

**Figura 6. Perfiles de diversidad taxonómica de las lagunas estudiadas.**

central zone of the wetlands which are dry in summer. The most important was Phyla nodiflora, which was present in 9 wetlands and had an importance value of 18.38. The next highest in importance were *Gnaphalium cymatoides* (7 wetlands, importance value 14.38) and *Centipeda elatinoides* (8 wetlands, importance value 12.36). It is possible that these ephemeral wetland specialists are dispersed from the native micro vernal pools present in the neighbourhood and described by Ramírez *et al.* (1994).

The vast majority of the wetland flora were

dry land plants or wetland generalists (in both cases 39 species, corresponding to 44.8 % of the total species number).

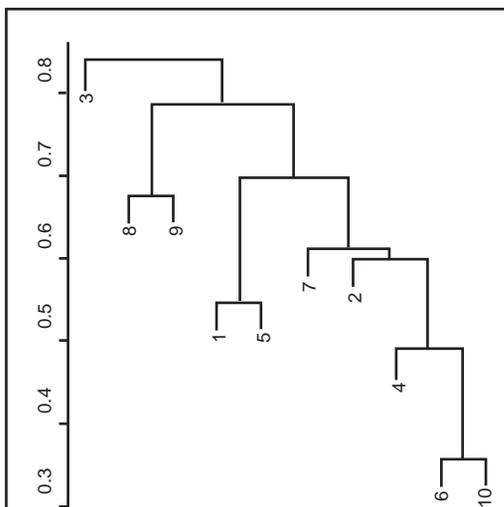
#### Plant diversity of the studied wetlands

A first analysis of the plant species diversity of the wetlands can be made with the species number, also called alpha diversity (Whittaker 1972). The wetland number 9 had the lowest species number (13 species, see also Table 7), whilst the number 4 had the highest alpha diversity (36 species). However, the relative diversity did not remain constant when considering the taxa at different levels (genera and families, Figure 6).

Comparing the floristic composition between wetlands (beta diversity sensu Whittaker 1972), we found a high degree of dissimilarity. In the dendrogram resulting from the clustering analysis (Figure 7) we obtained 3 clusters at a distance of about 0.7; the first cluster consists of wetland 3 only, the second wetlands 8 and 9, and the third consists of the rest of the wetlands. However the last cluster shows a high degree of heterogeneity. We found no correlation between the distance between wetlands and their similarity (Figure 8).

All of the regression models of the species number versus wetland area and number of present communities following the power model (Arrhenius 1921) were not significant, including the single models of wetland area ( $R^2 = 0.029$ ,  $p > 0.05$ ) and number of communities ( $R^2 =$

**Figure 7. Dendrogram of the agglomerative hierarchical cluster analysis using complete linkage and the Jaccard-index as a similarity measure. Figura 7. Dendrograma de la clasificación jerárquica usando el algoritmo “complete linkage” y el índice de Jaccard como medida de similitud.**



0.322,  $p > 0.05$ ) as well as the model including both parameters ( $R^2 = 0.384$ ,  $p > 0.05$ ).

### Ordination analysis

The wetlands in the ordination diagram (Figure 9) showed a high degree of dissimilarity according to their distribution. Extreme cases were represented by the wetlands number 3 and 8 that lie more separated from the rest of the wetlands. The distribution of the plant communities in the diagram also showed a high level of dispersion.

The proportion of therophyte, hemicryptophyte and adventive species were shown as vectors. The proportion of hemicryptophytes (see also Table 8) had the highest correlation with the ordination of the wetlands, whereas the lowest correlation was shown by the therophytes. Therophytes and hemicryptophytes were negatively correlated with each other; and they were poorly correlated with introduced species.

**Table 8. Correlation coefficients between the ordination axes and the proportion of therophytes, hemicryptophytes and introduced plants in the vegetation and for the presence of plant communities in the studied wetlands.**

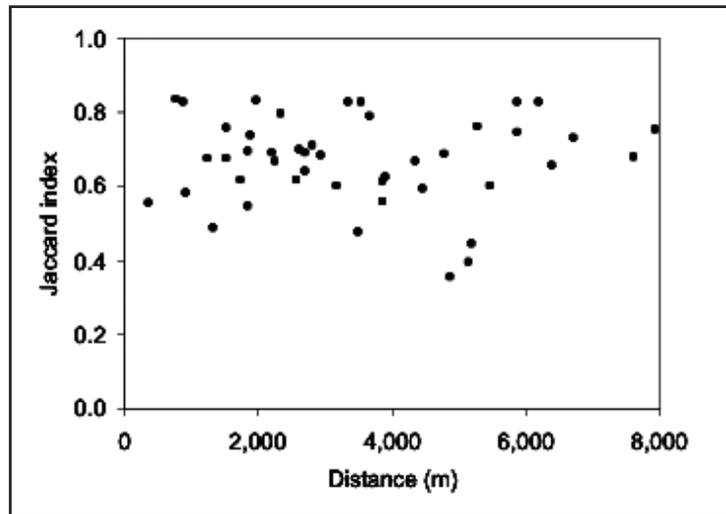
**Cuadro 8. Coeficientes de correlación entre las dimensiones de ordenación y la proporción de terófitas, hemicriptófitas y adventivas en la vegetación y la presencia de comunidades vegetales en las lagunas muestreadas.**

Dimensions	NMDS 1	NMDS 2	NMDS 1 + 2
Proportion of ...	Pearson correlations		
therophytes	0.297	0.421	0.478
hemicryptophytes	-0.824	-0.367	-0.891
introduced	-0.724	0.580	-0.294
Communities	Spearman rank-correlations		
Au	-0.722	0.494	-0.114
EL	0.406	0.522	0.406
Em	-0.266	0.038	-0.038
Ep	-0.104	0.174	-0.174
GM	0.522	-0.058	0.522
GP	-0.342	0.418	0.190
JC	-0.058	-0.406	-0.406
Jp	-0.284	-0.071	-0.071
LS	0.522	-0.058	0.522
MA	-0.355	-0.142	-0.142
Ph	-0.174	0.000	0.000
Pp	0.406	0.522	0.406

Community abbreviations are shown in Table 1.

**Figure 8. Floristic similarity between wetlands (pairwise comparison by Jaccard-index) versus distance between compared wetlands.**

**Figura 8. Similitud florística entre las lagunas (comparaciones pareadas usando el índice de Jaccard) en función a la distancia entre los humedales comparados.**



## DISCUSSION

### Wetland area and connectivity in the determination of species richness

As has been shown to be the case for Chilean grasslands (Oberdorfer 1960) and like Californian vernal pools (Barbour *et al.* 2005), the wetlands near Temuco were floristically poor. They reached a mean species density of only 8.4 species in 1,000 m<sup>2</sup>. Nevertheless, the area of the wetlands did not play an important role in the determination of the species number. Normally an analysis of the species-area relationship on a small scale results in low correlations, a phenomenon known as the small island effect (Lomolino y Weiser 2001). However, Alvarez (2008) reported a weak but significant correlation between species richness and area in smaller vernal pools (about 1.5 m<sup>2</sup>) near Temuco.

The fragmentation of this kind of habitat and the strong contrast of the environmental conditions with the surrounding upland (Holland y Jain 1981, Deil 2005) could result in a barrier for the dispersal between ponds. Moreover, seasonal wetland species normally have adaptations for restricted dispersal (Zedler 1990, Alvarez 2008). Under the scenario of restricted dispersal of species between wetlands, a higher floristic similarity was expected between wet-

lands closer together than between those further apart. This hypothesis was rejected as a result of the lack of correlation between distance and the similarity of the wetlands (Figure 8). An accidental dispersal of diaspores by water birds and livestock (diszoochory sensu Dansereau y Lems 1957) could produce a broad dispersal of the wetland species throughout the whole study area. Dispersal by epizoochorous mechanisms is not always restricted to diaspores with morphological adaptations such as hooks or viscous appendices, as demonstrated by Ramírez *et al.* (2003) in Southern Chilean grasslands.

### Within wetland diversity

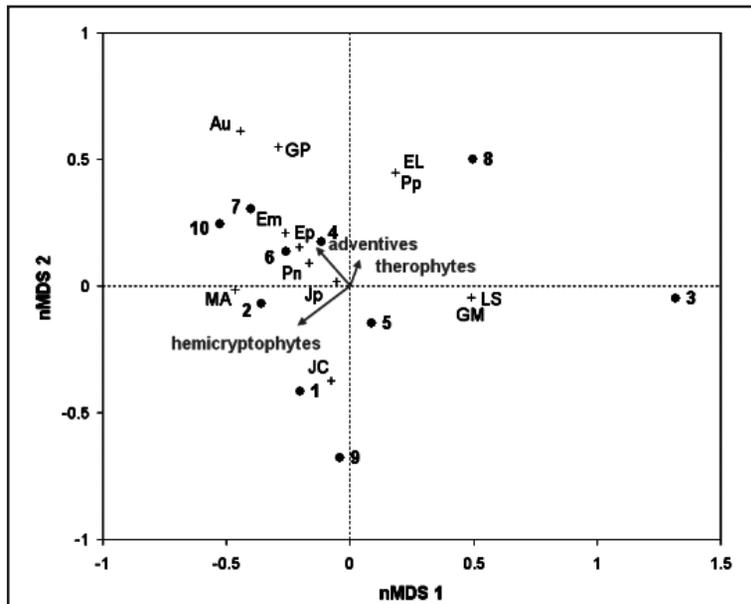
As a part of this study, two aspects of the so called within wetland diversity were analysed: 1) The change in diversity over different taxonomic levels (species, genera and families; Feoli y Scimone 1984). 2) The vegetation mosaics present in each wetland (Barbour *et al.* 2003).

In the first case, different tendencies in the change of diversity across taxonomic levels were found. For example, wetland number 8 was the richest wetland at the family level (Figure 6), but not at the species level. Only wetland number 9 remained the poorest at all taxonomical levels.

In the second case, the presence of different

**Figure 9.** Ordination diagram of the temporary wetlands (●) using a non-metric multidimensional scaling (nMDS) and the Bray-Curtis-index of dissimilarity. Plant communities (+) and proportion of indicator plants (represented as vectors) are added through post-hoc correlations. Stress = 10.10. Abbreviation of the plant communities are shown in Table 1.

**Figura 9.** Ordenación de las lagunas temporales (●) usando el método “non-metric multidimensional scaling” (nMDS) y el índice de disimilitud de Bray-Curtis. Las comunidades vegetales (+) así como también la proporción de plantas indicadoras (representadas por vectores) fueron agregadas usando correlaciones post-hoc. Stress = 10,10. Las abreviaciones de las comunidades vegetales se presentan en el Cuadro 1.



communities within the wetlands was very variable (Table 7). Surprisingly the number of communities in the wetlands was not correlated with the species number. This variability was not only reflected in the number of communities but by the community composition of each wetland (details published by San Martín *et al.* 1998). Similar results have been obtained analysing Californian vernal pools at a larger geographic scale (Barbour 2003).

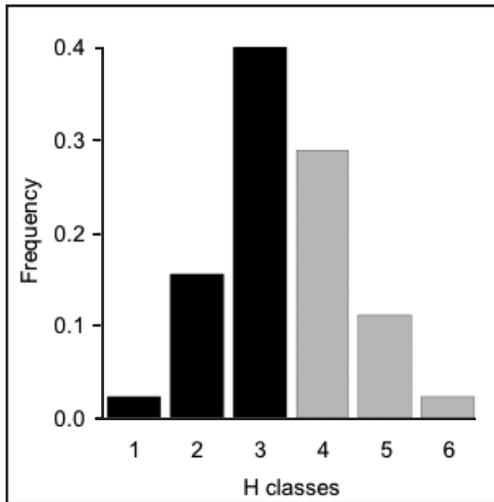
### Disturbance effects

Because all of the studied wetlands are anthropogenic in origin, all are the result of disturbance (deforestation). In addition, the seasonality in the environmental conditions that oscillate between the extremes of total drought and flooding could be interpreted as a natural disturbance, as it implies the frequent death of almost all of the aerial part of the vegetation (Deil 2005). A continual disturbance is provoked by the use of

these wetlands as watering and grazing places. This factor could produce effects through grazing, trampling and eutrophication as a result of waste deposition in the wetlands. Manure transported from the surrounding cultivated areas has an additional effect that contributes to their eutrophication.

The high number of introduced species and their high frequency around the wetlands (*e. g.* *Mentha pulegium*, *Leontodon taraxacoides* and *Polygonum persicaria*; see also Table 3) indicate both the secondary anthropogenic origin and the strong disturbance effect of land use on these wetlands (Hauenstein *et al.* 1988, Ramírez *et al.*, 1991).

The vectors used in the nMDS (Figure 9) as indicators of disturbance show a disturbance gradient from the right-bottom corner (low disturbance) to the left-top corner (high disturbance). According to this gradient, wetland number 3 has the lowest disturbance level, while wet-



**Figure 10. Distribution of homogenization indices (H) among pairs of wetlands. Black bars represent differentiation effect, while grey bars represent homogenization effect. H classes: 1 (-0.15 to -0.1), 2 (-0.1 to -0.05), 3 (-0.05 to 0), 4 (0 to 0.05), 5 (0.05 to 0.1) and 6 (0.1 to 0.5).**

**Figura 10. Distribución de los índices de homogenización (H) comparando pares de lagunas. Las barras negras representan efectos de diferenciación, mientras que las barras grises representan efectos de homogenización. Clases de H: 1 (-0.15 a -0.1), 2 (-0.1 a -0.05), 3 (-0.05 a 0), 4 (0 a 0.05), 5 (0.05 a 0.1) y 6 (0.1 a 0.5).**

lands number 10 and 7 have the highest level. At the high disturbance end of the gradient species number becomes also high, together with the importance of introduced species. These results contradict the findings of Ramírez *et al.* (1992), who observed a reduction in the species richness with disturbance. They also contradict the “intermediate disturbance hypothesis” (Connell 1978) that predicts a unimodal response by the species number (Grace 1999). But this interpretation does not represent a total agreement with the reality: wetland number 8, for example, is the only one with permanent water. On the other hand, wetland number 3 is intensively used as a watering place for cattle which implies a high level of eutrophication. According to our observations in 1996 and 1997, wetlands 3 and 9 endured a longer flooding period than the rest. Also, in wetland number 3 the aquatic plants reached their highest im-

portance. Because of this, it is probable that the above-mentioned gradient in reality indicates a gradient of seasonality rather than disturbance, starting in the right-bottom corner (near to permanent flooding) moving to the left-top corner (near to terrestrial). This suggestion is confirmed by the location of the plant communities in the ordination diagram. Moreover, following Crow (1993), diversity increases as a response to an alternating wet-dry climate, explaining the increase in species number with seasonality in the ordination diagram.

The proportion of introduced species was directly correlated with alpha diversity ( $R^2 = 0.716$ ,  $p < 0.01$ ), however, its effects on the beta diversity actually have an homogenization effect. The homogenization index of Qian y Ricklefs (2006) was calculated, making all possible pair-wise comparisons and calculating the Jaccard index of total species composition ( $J_{total}$ ) and the composition of native species ( $J_{native}$ ). The homogenization index (H) results from the following formula:  $H = J_{total} - J_{native}$ . About 60 % of all these comparisons had negative values (Figure 10), which indicates that there was a weak tendency to homogenization through introduced species.

## CONCLUSIONS

It is concluded that the area of the studied seasonal wetlands does not play any role in the determination of their species richness or the number of communities present in them. The within wetland diversity was also responsible for the high heterogeneity in the species compositions of the wetlands.

The floristic similarity between wetlands (beta diversity) was not related to the distance between them. This may be due to their heterogeneity and the lack of restrictions for broad dispersal of the plant species, at least at the geographical scale of this work.

It is difficult to estimate the effect of disturbance on the species richness using ecological indicators. In this study, the nMDS ordination did not reflect all aspects of disturbance in the ordination diagram, relating to the importance of

hemicryptophytes, therophytes and introduced species. It is possible that factors not measured in this research, like seasonality and the nutrient content of soil and water, were also related to disturbance and important in the determination of the species composition of the wetlands.

Finally, the importance of introduced plants was directly correlated with the species richness of the wetlands; together they produced a weak homogenization of the species composition between wetlands.

The high importance of introduced species and the low amount of ephemeral wetlands specialists confirms their secondary, anthropogenic character.

## ACKNOWLEDGEMENTS

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**Appendix: Scientific names, families, life-forms (lf), status (S), frequencies in the pools (F), and importance values (IV) of the flora of the anthropogenic vernal pools (Temuco, Chile).**

Scientific name	Family	lf	S	F	IV
<b>MAGNOLIOPSIDA</b>					
<i>Achillea millefolium</i> L.	Asteraceae	H	a	1	0.63
<i>Aster vahlII</i> (Gaudich.) Hook. et Arn.		C	n	3	1.89
<i>Baccharis sagittalis</i> (Less.) DC.		P	n	1	0.63
<i>Callitriche hermaphroditica</i> L.	Callitricheaceae	Cr	a	1	1.26
<i>Callitriche palustris</i> L.		T	a	1	0.63
<i>Callitriche terrestris</i> Raf.		Cr	n	2	5.11
<i>Centipeda elatinoides</i> (Lees.) Benth. et Hook. f. ex O. Hoffm.	Asteraceae	H	n	8	12.36
<i>Chamomilla recutita</i> (L.) Rauschert		T	a	2	1.89
<i>Cirsium vulgare</i> (Savi) Ten.		T	a	2	1.44
<i>Crassula peduncularis</i> Reiche	Crassulaceae	Cr	n	1	2.53
<i>Crepis capillaris</i> (L.) Wallr.	Asteraceae	T	a	2	1.26
<i>Cuscuta suaveolens</i> Ser.	Cuscutaceae	T	n	2	1.26
<i>Daucus carota</i> L.	Apiaceae	T	a	1	0.63
<i>Dichondra sericea</i> Sw.	Convolvulaceae	H	n	3	4.42
<i>Eryngium humifusum</i> Clos	Apiaceae	H	n	2	2.19
<i>Eryngium pseudojunceum</i> Clos		H	n	7	8.40
<i>Gnaphalium americana</i> (Mill.) Wedd.	Asteraceae	H	n	4	3.16
<i>Gnaphalium spiciformis</i> (Sch. Bip.) Cabrera		H	n	2	1.26
<i>Geranium core-core</i> Steud.	Geraniaceae	T	n	2	1.26
<i>Glinus radiatus</i> (Ruiz et Pav.) Rohrb.	Molluginaceae	T	n	3	4.42
<i>Gnaphalium cymatoides</i> Kunze ex DC.	Asteraceae	T	n	7	14.38
<i>Gratiola peruviana</i> L.	Scrophulariaceae	C	n	9	17.62
<i>Heptyotis salzmännii</i> (DC.) Steud.	Rubiaceae	H	n	3	1.89
<i>Hydrocotyle marchantioides</i> Clos	Hydrocotylaceae	H	n	2	3.18
<i>Hypochaeris radicata</i> L.	Asteraceae	H	a	6	5.05
<i>Leontodon taraxacoides</i> (Vill.) Mérat		H	a	8	26.66
<i>Limosella australis</i> R.Br.	Scrophulariaceae	Cr	n	1	3.16
<i>Lotus corniculatus</i> L.	Fabaceae	H	a	1	0.63
<i>Lotus uliginosus</i> Schkuhr		H	a	8	17.65
<i>Ludwigia pepioides</i> (Humb., Bonpl. et Kunth) P.H. Raven	Onagraceae	Cr	n	1	5.56
<i>Lythrum portula</i> (L.) D.A. Webb	Lythraceae	Cr	a	4	7.90
<i>Mentha pulegium</i> L.	Lamiaceae	C	a	9	40.48
<i>Modiola caroliniana</i> (L.) G. Don	Malvaceae	H	a	1	0.63
<i>Muehlenbeckia hastulata</i> (Sm.) I.M. Johnston	Polygonaceae	P	n	1	0.63
<i>Myosotis arvensis</i> (L.) Hill.	Boraginaceae	T	a	2	1.89
<i>Myrcogenia esucca</i> (DC.) O. Berg	Myrtaceae	P	n	3	1.89
<i>Myriophyllum aquaticum</i> (Vell.) Verdc.	Haloragaceae	Cr	n	1	1.26
<i>Navaretia involucreata</i> Ruiz et Pav.	Polemoniaceae	T	n	2	4.60
<i>Oxalis corniculata</i> L.	Oxalidaceae	T	a	2	1.89
<i>Parentucellia viscosa</i> (L.) Caruel	Scrophulariaceae	T	a	1	0.63
<i>Phylla nodiflora</i> (L.) Greene	Verbenaceae	H	a	9	18.38
<i>Plantago lanceolata</i> L.	Plantaginaceae	H	a	2	3.16
<i>Polygonum aviculare</i> L.	Polygonaceae	C	a	1	0.63
<i>Polygonum hydropiperoides</i> F. Michx.		H	a	10	24.04

## Appendix (continuation)

Scientific name	Family	Lf	S	F	I.V.
<i>Polygonum persicaria</i> L.	Polygonaceae	T	a	2	2.53
<i>Prunella vulgaris</i> L.	Lamiaceae	C	a	5	5.68
<i>Ranunculus bonariensis</i> Poir.	Ranunculaceae	T	n	1	0.63
<i>Rorippa palustris</i> (L.) Besser	Brassicaceae	T	a	1	0.63
<i>Rubus constrictus</i> P.J.Müll. et Lefevre	Rosaceae	P	a	5	5.05
<i>Rumex acetosella</i> L.	Polygonaceae	H	a	5	8.21
<i>Rumex conglomeratus</i> Murray		H	a	7	11.36
<i>Spergularia rubra</i> (L.) J.Presl et C.Presl	Caryophyllaceae	C	a	6	7.68
<i>Trifolium repens</i> L.	Fabaceae	H	a	2	1.26
<i>Utricularia gibba</i> L.	Lentibulariaceae	Cr	n	1	2.53
<i>Veronica anagallis-aquatica</i> L.	Scrophulariaceae	Cr	a	1	1.26
LILIOPSIDA					
<i>Agrostis capillaris</i> L.	Poaceae	H	a	8	21.39
<i>Alisma plantago-aquatica</i> L.	Alismataceae	Cr	a	1	2.53
<i>Anthoxanthum utriculatum</i> (Ruiz et Pav.) Y. Schouten et Veldkamp	Poaceae	H	n	4	4.51
<i>Arrhenatherum elatius</i> (L.) P.Beauv. ex J.Presl et C.Presl		H	a	1	0.63
<i>Briza minor</i> L.		T	a	1	0.63
<i>Carex riparia</i> Curtis	Cyperaceae	H	n	1	1.19
<i>Cynosurus echinatus</i> L.	Poaceae	T	a	2	1.26
<i>Cyperus conceptionis</i> Steud.	Cyperaceae	H	n	1	1.26
<i>Cyperus eragrostis</i> Lam.		H	n	3	2.53
<i>Cyperus reflexus</i> Vahl		H	n	8	15.78
<i>Echinochloa crus-galli</i> (L.) P.Beauv.	Poaceae	T	a	1	0.63
<i>Eleocharis macrostachya</i> Britton	Cyperaceae	H	n	6	14.85
<i>Eleocharis pachycarpa</i> E.Desv.		H	n	9	25.18
<i>Glyceria multiflora</i> Steud.	Poaceae	T	n	7	6.69
<i>Holcus lanatus</i> L.		H	a	5	7.14
<i>Juncus bufonius</i> L.	Juncaceae	T	a	1	1.26
<i>Juncus imbricatus</i> Laharpe		H	n	5	7.43
<i>Juncus microcephalus</i> Humb., Bonpl. et Kunth		H	n	6	7.18
<i>Juncus pallescens</i> Lam.		H	n	1	1.29
<i>Juncus procerus</i> E.Mey.		H	n	9	21.84
<i>Juncus stipulatus</i> Nees et Meyen		T	n	1	0.63
<i>Nothoscordum gramineum</i> (Sims) Beauverd	Liliaceae	Cr	n	1	1.26
<i>Panicum capillare</i> L.	Poaceae	T	a	2	1.26
<i>Paspalum distichum</i> L.		H	a	2	1.26
<i>Piptochaetium montevidense</i> (Spreng.) Parodi		H	n	1	0.63
<i>Polypogon australis</i> Brongn.		H	n	2	3.79
<i>Potamogeton pusillus</i> L.	Potamogetonaceae	Cr	n	1	1.25
<i>Sagittaria montevidense</i> Cham et Schitdl.	Alismataceae	Cr	n	1	8.44
<i>Scirpus californicus</i> (C.A.Mey.) Steud.	Cyperaceae	Cr	n	1	2.94
<i>Setaria parviflora</i> (Poir.) Kerguelen	Poaceae	H	a	4	3.79
<i>Sisyrinchium graminifolium</i> Lindl.	Iridaceae	Cr	n	1	0.63
<i>Vulpia bromoides</i> (L.) Gray	Poaceae	T	a	1	0.63

Life forms: phanerophytes (P), chamaephytes (C), hemicryptophytes (H), cryptophytes (Cr) and therophytes (T). Status: natives (n), introduced (a)