*WETLANDS*, Vol. 19, No. 3, September 1999, pp. 517–534


# FLORISTIC COMPARISON OF FRESHWATER WETLANDS IN AN URBANIZING ENVIRONMENT

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*Abstract:* We evaluated the floristic condition of freshwater palustrine wetlands dominated by wet meadow, emergent marsh, aquatic vegetation, or open water within the rapidly urbanizing area of Portland, Oregon, USA by (1) characterizing plant species richness (presence/absence) and composition of naturally occurring wetlands (NOWs) and mitigation wetlands (MWs) and (2) identifying relationships between floristic characteristics and variables describing land-use, site conditions, and mitigation activities. Data were collected on 45 NOWs and 51 MWs. Overall species richness was high (365 plant taxa), but more than 50% of the species present on both NOWs and MWs were introduced. Only 14 species occurred on more than half the sites, and nine of them were invasive introduced species. The mean number of native species per site did not differ between land-use categories (ANOVA, F = 0.62 at 3 and 88 df, p = 0.6031); however, wetlands surrounded by agricultural and commercial/industrial/transportation corridor uses had more introduced species per site than wetlands surrounded by undeveloped land (Fishers Protected LSD at 88 df, p ≤ 0.05). Although overlapping in floristic composition, NOWs and MWs had significantly different (MRPP, p < 0.0001) species assemblages that were identified using TWINSPAN. MRPP analyses for all sites showed that watershed, land-use, HGM class, percent cover of water, and MW age were significantly related to the floristic composition of the study wetlands. Canonical correspondence analyses further revealed that the primary gradient for species distribution in NOWs was related to moisture; the secondary gradient was related to land-use. The primary gradient also described a strong relationship between percent cover of water and HGM class. For MWs, the primary gradient was related to watershed location and surrounding land-use; the secondary gradient was related to percent cover of water and MW age. Most MWs (44 out or 51 sites) were depressions in various settings, so while HGM class separates NOWs from MWs, it does little to distinguish MW assemblages. Our results show that wetlands in the urbanizing study area are floristically degraded. Further, current wetland management practices are replacing natural marsh and wet meadow systems with ponds, resulting in changes in the composition of plant species assemblages.

*Key Words:* biodiversity, canonical correspondence analysis (CCA), hydrogeomorphic classes (HGM), introduced species, mean similarity dendrograms, multiple response permutation procedures (MRPP), native species, introduced species, Oregon, USA, TWINSPAN, wetland mitigation, urban ecosystems

## INTRODUCTION

The effects of urban-induced degradation on natural ecosystems are increasingly recognized as critical areas of ecological research (Limburg and Schmidt 1990, Matson 1990, McDonnell and Pickett 1990, Blair 1996). Recent work has shown that land-use patterns and degree of urbanization influence species composition of bird (Blair 1996), amphibian (Richter and Azous 1995), forest (Rudnicky and McDonnell 1989, Pouyat et al. 1994, Medley et al. 1995), and wetland plant (Erhenfeld and Schneider 1991, Cooke and Azous 1993) communities. Although often altered or degraded, urban natural areas can provide valuable ecological and societal functions. Metropolitan wetlands, in particular, support aquatic and terrestrial habitats and sustain many plant, invertebrate, and wildlife species, thus contributing to conservation of biodiversity through the maintenance of native biotic communities (Myers 1988, NRC 1995).

Despite their ecological importance, wetlands in urban areas frequently show signs of diminished structure and function. One of the most visible aspects of altered structure is the invasion of native communities by non-native plant species (Kusler 1988, McColligan and Kraus 1988, Ehrenfeld and Schneider 1993). Although the threat to native diversity posed by introduced species is well-documented, the extent to which the flora of wetlands in urban settings is diluted by introduced species has received less attention. For some wetland ecosystems, the influx of introduced plant species has been shown to be associated with altered hydrology and increasing intensity of surrounding land-use (Cooke and Azous 1993, Ehrenfeld and Schneider 1993, Taylor 1993, Houck 1996). Intensified land-use adjacent to wetlands or in associated stream drainage ways can result in physical changes to wetland environments that may affect plant species assemblages. In particular, increased impervious surface in surrounding areas has been linked to altered hydrologic regime and increased water-level fluctuation (Taylor 1993, Mitsch and Wilson 1996), increased sedimentation (Simenstad and Thom 1996), and increased runoff of contaminated storm water (Booth 1991, Booth and Jackson 1994, Schueler 1994).

In addition to the effects of adjacent land-use, urban wetlands are influenced by regulatory practices dictated by federal legislation. Wetlands in the United States are protected under Section 404 of the U.S. Clean Water Act, which requires mitigation of adverse environmental impacts to wetlands due to activities associated with development (U.S. Department of the Army and U.S. Environmental Protection Agency 1990). Mitigation can include restoration or enhancement of existing degraded wetlands or creation of new wetlands from uplands (Kruczynski 1990). A study of regulatory decisions in Oregon and Washington, USA showed that most wetland losses or alterations and subsequent mitigation activities occurred in urban or urbanizing areas (Kentula et al. 1992a). Further, these activities involved net loss of wetland area, and mitigation often resulted in different types of wetlands than those destroyed (Kentula et al. 1992a). Although similar changes in wetland resources have been documented elsewhere (Holland and Kentula 1992, Sifneos et al. 1992a, b), the ecological effects of mitigation practices, particularly on the regional floristics, are largely unknown.

We examined the floristic characteristics of freshwater palustrine wetlands dominated by wet meadow, emergent marsh, aquatic vegetation, or open water within the Portland, Oregon metropolitan area. We hypothesized that degree of nativeness and floristic composition of the plant community would be related to the environmental conditions, surrounding land-use, and mitigation activities associated with the study wetlands. Specific objectives were to (1) characterize plant species richness and composition of naturally occurring wetlands (NOWs) and mitigation wetlands (MWs) in an urbanizing area and (2) identify relationships between floristic characteristics and variables describing land-use, site conditions, and mitigation activities.

## METHODS

### Study Area and Site Selection

The study area was defined by the Portland, Oregon Urban Growth Boundary (DLCD 1992, Metro 1997) that separates land designated for urbanization from rural land (Figure 1) and is located in the Willamette Valley Plains Subecoregion (Clarke et al. 1991). The area surrounding Portland and its neighboring municipalities is occupied primarily by agricultural use, old fields, or undeveloped land. Lands near the urban growth boundary and along major transportation corridors, however, are receiving increased pressure for conversion to urban uses, resulting in the loss of numerous wetlands (Holland et al. 1995). Many of the remaining urban wetlands are small and isolated from more extensive wetland systems or floodplains and from surrounding uplands.

Study sites were small ($\leq$ 2 ha) palustrine wetlands (Cowardin et al. 1979) dominated by some combination of wet meadow, emergent marsh, and aquatic vegetation. This group was chosen because it represents wetlands historically most common in the Willamette Valley (Davis 1995, Guard 1995) and those most frequently destroyed and required as mitigation in the Portland area and the State of Oregon (Kentula et al. 1992a, b). Recent National Wetland Inventory maps, based on 1981 and 1982 aerial photographs, were used to identify all existing NOWs of the appropriate size and type. NOWs were chosen in a stratified random sample based on proportional representation of undeveloped (UND), agricultural (AG), residential (RES), commercial, industrial, and transportation corridor land-uses. Commercial, industrial, and transportation corridor were later pooled into a single class (CIT). All MWs of the appropriate size and type were identified from the records of the Oregon Division of State

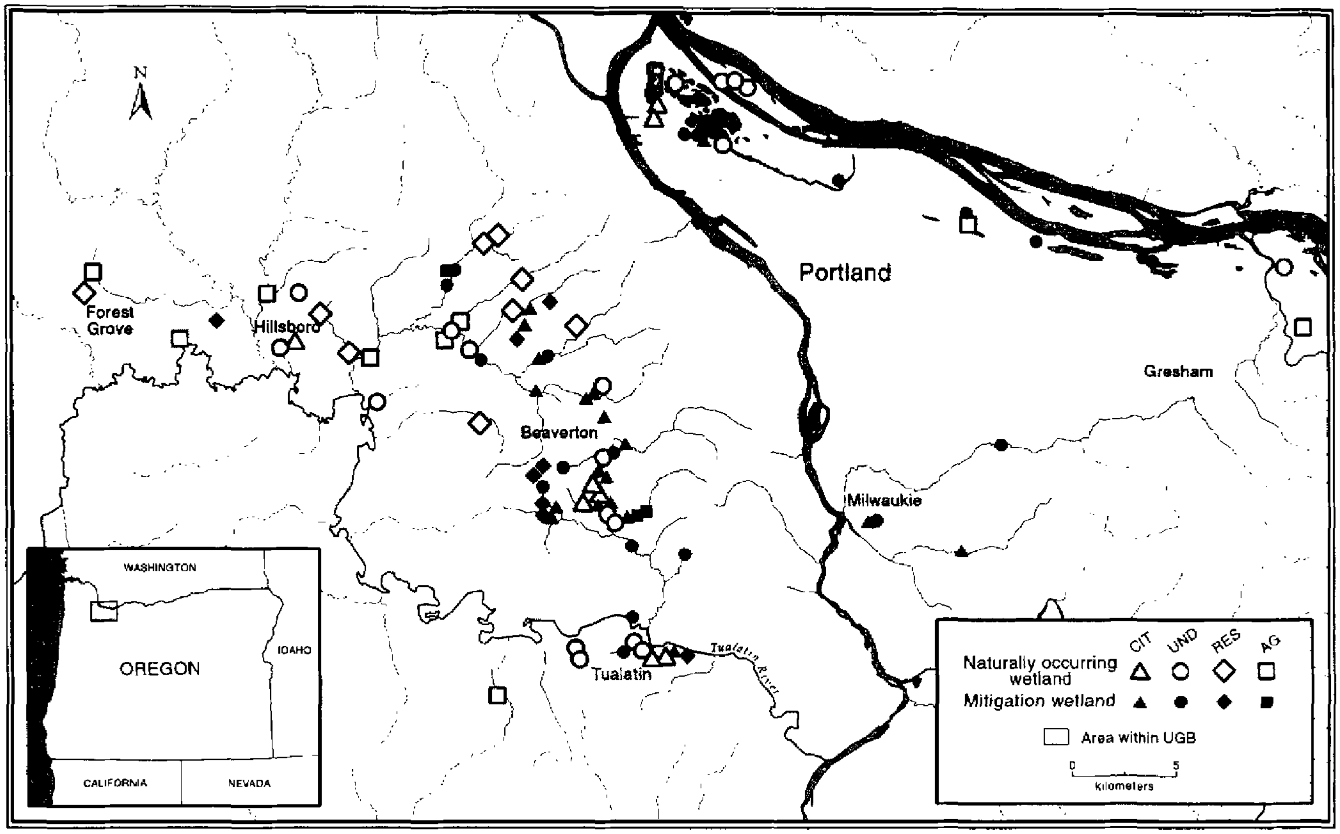



Figure 1. Map of the Portland, Oregon metropolitan area showing the locations and surrounding land-use (CIT = commercial/industrial/transportation corridor, UND = undeveloped, RES = residential, AG = agricultural) of the naturally occurring wetland (NOWs) and mitigation wetlands (MWs) studied.

Lands (ODSL), which included information on wetland losses and mitigation permitted under federal regulations, as well as decisions involving small or isolated wetlands covered under the jurisdiction of the State of Oregon (Administrative Rules 1986, Oregon Statutes 1989). Our final sample of 96 wetlands included 45 NOWs and 51 MWs, which comprised 62% of the NOWs and 98% of the MWs in the target group (Magee et al. 1995). The MWs ranged in age from 1 to 11 years, with a mean age of 5 years. Among NOWs meeting study criteria, nine were excluded in the random selection procedure and 19 were dropped due to access constraints or hazardous conditions. Only one MW meeting selection criteria was excluded due to safety considerations.

## Floristic Sampling and Nomenclature

Plant species presence/absence data were collected in 1-$m^2$ plots located along parallel transects of a systematic grid covering each site for 93 of the wetlands (Magee et al. 1993). Plots were spaced along the transects at intervals of 1, 3, 6, or 9 m, depending on wetland size (mean = 0.37 ha), resulting in an average of 57 plots/site. Three MWs had vegetation that occurred as a very narrow, non-zonal band (1–2 m wide) of plants along the perimeter of a pond or a series of ditches. For these sites, the number of vegetated plots intersecting the transect grid was very low. Therefore, additional transects were placed within and parallel to the band of vegetation, and plots were systematically located along transects at the same interval used on the grid (Magee et al. 1993). Data were collected from 22 June through 12 August 1993, when the greatest number of species would be at phenological stages suitable for identification. Species accumulation curves (bootstrapping technique, PC-ORD© version 3.15, McCune and Mefford 1997) indicate that sample size was sufficient to encounter most species occurring at each site. Nevertheless, it is probable that some infrequent taxa and some early spring ephemeral species were not observed.

Among vascular taxa, 315 (86%) were identified to species, 44 (12%) to genus, and 1 (0.3%) to family. Among non-vascular taxa, *Chara* sp. was identified to genus, and others were grouped as bryophytes, fungi, algae, or lichen. For all taxa observed in the study, scientific names, authorities, and the number of occur-

Table 1. Description of environmental variables.

| Percent Cover of Water | $\bar{x}$ % Cover of Water Per Site = Σ % Cover Water in All Plots/Total Number Plots |
|---|---|
| Predominant Land-use: | |
| UND - Undeveloped | Natural vegetation, old fields, and surface water (lake or stream). |
| RES - Resedential | Single and/or multi-family residences, light-duty paved roads. |
| AG - Agricultural | Cropland, orchard, pasture, plowed fields, and unpaved roads used primarily for access to agricultural fields. |
| CIT - Commercial/industrial/transportation corridor | Commercial and industrial use and highways, roads, and railroads. |
| Wetland Hydrogeomorphic (HGM) Class§: | |
| RIV - Riverine | Occurs in flood plains and riparian corridors in association with a stream channel. |
| SL - Slope | Occurs on sloping land where there is discharge of ground water to the land surface; lacks contours that would permit storage of water. |
| LAC - Lacustrine-fringe | Adjacent to lakes where the water elevation of the lake maintains the wetland water table. |
| DEP - Depression | Occurs in topographic depressions with contours that allow surface-water accumulation. |
| DR - Depression-in-riverine-setting | Human-made depression placed in a riverine setting; hydrology is kept separate from the stream except during high water events by a berm. |
| DSL - Depression-in-slope-setting | Human-made depression placed on sloping land with ground-water discharge to the surface; contours of the depression permit the accumulation and storage of water. |
| ISD - In-stream-depression | Human-made depression with semi-closed contours placed within the channel of a lower order stream. |

§ Gwin et al. 1999.

rences on NOWs and MWs are provided in *Floristic Data for 96 Palustrine Emergent Wetlands in Portland, Oregon* (FDPEM-Portland 1999) available at http://www.epa.gov/emap, and hosted by the United States Environmental Protection Agency—EMAP Data. Nomenclature follows *A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland* of the Biota of North America Project (BONAP 1996). All taxa were assigned to categories describing their ecological status based on native or introduced origin (Hitchcock and Cronquist 1973, Guard 1995), United States Fish and Wildlife Service (USFWS) Wetland Indicator Categories (Reed 1988, 1993), and designation as invasive species (FDPEM-Portland 1999). Plant species characterized as invasive or noxious weeds were identified using information from local floras and noxious weed lists or floras describing wide-spread introduced species (Hitchcock and Cronquist 1973, Hawkes et al. 1989, Taylor 1990, Washington State Department of Agriculture 1992, U.S. Congress, Office of Technology Assessment 1993, Oregon State Department of Agriculture 1994, Guard 1995, Houck 1996 and Whitson et al. 1996).

### Environmental Variables

Boundaries for each site were established based on shifts from wetland to upland vegetation and changes in slope between the wetland and the adjacent upland. Each site was surveyed, mapped, and then assigned to a predominant land-use class, based on the land-use with highest percent cover within a 100-m radius surrounding the wetland boundary, and to a regional hydrogeomorphic class (HGM) according to Gwin et al. (1999) (Table 1). Percent cover of water was estimated in each plot along the transect grid (Table 1) and used to estimate the extent of inundation during the growing season and as an indicator of water regime. The watershed (Upper Tualatin, Lower Tualatin, Willamette, Columbia) in which each study site occurred was identified from United States Geological Survey 1:24,000 topographic maps. Finally, the completion date for each MW was obtained from the ODSL files to determine its age.

### Data Analyses

Floristic composition of the study sites and relationships of floristic attributes or species groups to watershed, land-use, HGM classes, and percent cover of water were examined using a variety of univariate and multivariate analyses. Presence/absence data for all taxa ($n = 365$) were used in univariate analyses evaluating species richness and in comparisons involving native and introduced species. For multivariate analyses examining floristic composition, we excluded species that occurred on fewer than five sites to avoid potentially spurious results related to the presence of infrequent taxa (Gauch 1982). The resulting data set had 131 taxa. Univariate analyses were conducted using SAS statistical software, version 6.11; multivariate analyses, using PC-ORD© version 3.15 (McCune and Mefford 1997).

In the absence of historic floristic data for the Portland area, we used the occurrence of introduced plant species as an indicator of wetland stress (Keddy et al. 1993) and native biodiversity as an indicator of the quality, condition, and sustainability of an ecosystem (McColligan and Kraus 1988, Ehrenfeld and Schneider 1991, Noss and Cooperrider 1994, Andreas and Lichvar 1995). Occurrence was defined as the presence of any species, taxon, or attribute (i.e., native/introduced or invasive species) at a site. Percent of native species (PN) of a wetland was calculated as *PN = (Number of native species/Total number of species) × 100.* PN was used in making standardized comparisons to assess the condition of the flora across NOWs and MWs. Differences in the richness of native or introduced species between land-use classes and wetland types (NOWs and MWs) were based on occurrence rather than PN because occurrence weights all species equally; thus, sites with comparable numbers of introduced species are invaded to the same extent (McIntyre et al. 1988). A square root transformation was applied to the variables to stabilize the variances when necessary.

We used two-way indicator species analysis (TWINSPAN), a hierarchic classification procedure (Hill 1979) that emphasizes gradient segmentation as a classification criterion rather than cluster seeking (Carleton et al. 1996) to identify groups of NOWs and groups of MWs with similar species assemblages. The validity of the TWINSPAN groupings were assessed using multi-response permutation procedures (MRPP) (Zimmerman et al. 1985, Biondini et al. 1988, McCune and Mefford 1997) and mean similarity dendrograms (Van Sickle 1997).

MRPP and mean similarity dendrograms were also used to evaluate the relationships between environmental variables and floristic composition. Sites were divided into groups based on the categories for watershed, land-use, and HGM class (Table 1). Percent water cover and age of MWs were converted into range classes, and sites were grouped accordingly. The hypothesis of no difference in floristic composition between the groups of sites was tested for each variable.

We further investigated relationships of floristic composition to environmental variables using canonical correspondence analysis (CCA), a gradient analysis technique that incorporates both species and environmental data (ter Braak 1986, 1987a, 1988, Palmer 1993). CCA was applied to two partitions of the data set (NOWs and MWs) in separate analyses to assess the relationships between the environmental variables and sites or species assemblages. Neither transformations nor down-weighting were applied to the species data, and CCA site scores were plotted as weighted means of the species scores so that the approximate floristic composition at the sites is represented on the biplots (ter Braak 1986). Site groupings identified by TWINSPAN were included on the resulting CCA biplots to evaluate the species assemblages relative to environmental gradients.

## RESULTS

Both NOWs and MWs had a mean of about 50% native species. Overall richness was high, with 306 species found on MWs, 274 species observed on NOWs, and a total of 365 plant taxa identified across all 96 study sites (FDPEM-Portland 1999). Only 95 taxa were found on 10 or more sites, and just 14 species occurred on more than half ($\geq$ 47) of the sites (Table 2). Nine of the 14 most common taxa (Table 2) were invasive introduced species. The most frequently encountered species, *Phalaris arundinacea,* was found on 89 sites (93% of the total). Five species are introduced pasture grasses, and three are invasive/introduced shrubs or forbs. The most frequently observed native species were a mixture of graminoids, small aquatic forbs, and a tall-emergent.

The influence of land-use on floristic condition was assessed by comparing mean occurrences for native, introduced, and invasive/introduced species (Table 3). No significant interaction existed between land-use and wetland type (NOW and MW) for the occurrence of native (ANOVA, $F = 0.46$ at 3 and 88 df, $p = 0.7122$), introduced (ANOVA, $F = 0.40$ at 3 and 88 df, $p = 0.7544$), nor invasive/introduced (ANOVA, $F = 1.47$ at 3 and 88 df, $p = 0.2270$) species. The mean number of native species per site was not significantly different between land-use categories (ANOVA, $F = 0.62$ at 3 and 88 df, $p = 0.6031$). However, there were significant differences in the occurrence of introduced species between UND and both AG and CIT land-uses. Wetlands surrounded by CIT averaged three more invasive/introduced species per site than wetlands surrounded by UND.

### Comparison of NOWs and MWs

Differences were observed in the floristic characteristics of NOWs and MWs. Mean percent native species was slightly greater across MWs (47 %) than NOWs (43 %) (ANOVA, $F = 3.80$ at 1 and 94 df, $p = 0.0542$). Similarly, mean species richness was signifi-

Table 2. Species found on ≥ 47 (> 50%) of the sites and common to naturally occurring wetlands (NOWs) and mitigation wetlands (MWs). United States Fish and Wildlife Service wetland plant indicator categories (Reed 1988, 1993): OBL = obligate wetland, FACW = facultative wetland, FAC = facultative, FACU = facultative upland.

| Species | NOWs (n) | MWs (n) | Total (n) | Growth Form |
|---|---|---|---|---|
| Introduced Species | | | | |
| *Phalaris arundinacea* (FACW) | 45 | 44 | 89 | Grass |
| *Holcus lanatus* (FAC) | 29 | 40 | 69 | Grass |
| *Agrostis gigantea* (FACW) | 24 | 38 | 62 | Grass |
| *Rubus discolor* (FACU) | 28 | 32 | 60 | Woody vine/shrub |
| *Festuca arundinacea* (FACU) | 20 | 34 | 54 | Grass |
| *Agrostis capillaris* (FAC) | 17 | 36 | 53 | Grass |
| *Solanum dulcamara* (FACW) | 23 | 25 | 48 | Vine |
| *Ranunculus repens* (FACW) | 21 | 27 | 48 | Forb |
| *Alopecurus pratensis* (FACW) | 22 | 25 | 47 | Grass |
| Native Species | | | | |
| *Juncus effusus* (FACW) | 27 | 48 | 75 | Rush |
| *Veronica americana* (OBL) | 17 | 37 | 54 | Forb |
| *Lemna minor* (OBL) | 20 | 34 | 54 | Floating aquatic |
| *Carex stipata* (OBL) | 18 | 31 | 49 | Sedge |
| *Typha latifolia* (OBL) | 14 | 33 | 47 | Tall emergent |

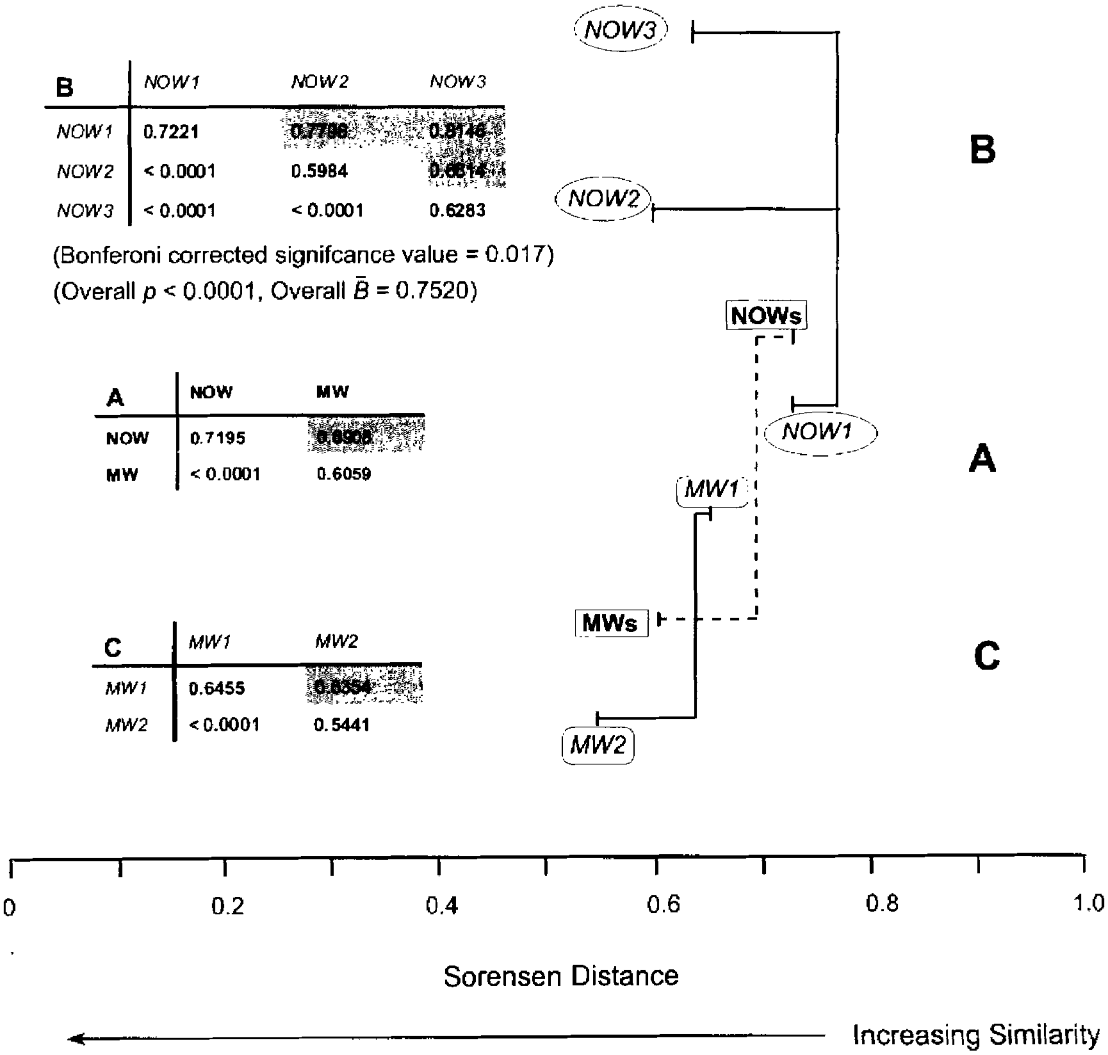
cantly higher on MWs ($\bar{x}$ = 41 species/site, range = 17–67) than on NOWs ($\bar{x}$ = 30 species/site, range = 6–68) (Wilcoxon Rank Sums, Z = −3.4503, p = 0.0006). Differences between NOWs and MWs in native, introduced, and invasive/introduced components of the flora were also significant (Table 3). Substantial overlap in floristic composition was noted, with 220 species found on both NOWs and MWs. Nevertheless, many species were unique to either NOWs (59, occurring at ≤ 6 sites) or MWs (86, occurring on ≤4 sites).

Differences in species distribution between NOWs and MWs were examined using MRPP and TWINSPAN. NOWs and MWs had significantly different (MRPP, p < 0.0001) floristic composition (Figure 2A). A mean similarity dendrogram was used to assess within- or between-group (NOW vs. MW) similarities (Figure 2A). The node of the dendrogram is plotted at the overall mean between-group distance ($\bar{B}$), and the branches representing each group terminate at the mean within-group distance ($\bar{W}_i$). NOWs and MWs shared on average 31% ($\bar{B}$ = 0.6908) of their species. The NOW and MW branch ends on the dendrogram show $\bar{W}_{NOW}$ = 0.7195 and $\bar{W}_{MW}$ = 0.6059. Since $\bar{W}_{MW} < \bar{B}$, MWs are floristically more similar to one another than they are to NOWs. MW site pairs shared approximately 40% ($\bar{W}_{MW}$ = 0.6059) of their species. In contrast, NOWs seemed to have greater between-site het-

Table 3. Comparison of mean species occurrences (mean ± SE) for native, introduced, and invasive/introduced species in each land-use category (UND = undeveloped, RES = residential, AG = agricultural, CIT = commercial/industrial/transportation corridors) and for naturally occurring (NOWs) and mitigation (MWs) wetlands. Note: invasive/introduced species are a subset of introduced species. Means within each column with the same letters are not significantly different§ (comparisons across columns are not meaningful).

| Predominant Land-use | Native | Introduced | Invasive/Introduced |
|---|---|---|---|
| UND (n = 39) | 15.8 ± 2.4 a | 14.0 ± 1.2 a | 7.0 ± 0.7 a |
| RES (n = 17) | 15.1 ± 1.6 a | 16.9 ± 1.8 a, b | 8.7 ± 0.9 a, b |
| AG (n = 12) | 17.8 ± 2.4 a | 21.3 ± 2.5 b | 9.3 ± 1.1 a, b |
| CIT (n = 28) | 15.9 ± 1.2 a | 19.1 ± 1.5 b | 9.8 ± 0.8 b |
| **Wetland Type** | **Native** | **Introduced** | **Invasive/Introduced** |
| NOWs (n = 45) | 12.6 ± 0.8 a | 14.6 ± 1.2 a | 7.0 ± 0.6 a |
| MWs (n = 51) | 18.9 ± 1.2 b | 19.0 ± 1.1 b | 9.6 ± 0.6 b |

§ Fisher's protected least significant difference (LSD) for pairwise comparison following ANOVA, p ≤ 0.05. A square root transformation was applied to stabilize variances.




| B | NOW1 | NOW2 | NOW3 |
|---|---|---|---|
| NOW1 | 0.7221 | 0.7798 | 0.8146 |
| NOW2 | < 0.0001 | 0.5984 | 0.6614 |
| NOW3 | < 0.0001 | < 0.0001 | 0.6283 |

(Bonferoni corrected signifcance value = 0.017)
(Overall $p < 0.0001$, Overall $\bar{B} = 0.7520$)

| A | NOW | MW |
|---|---|---|
| NOW | 0.7195 | 0.6908 |
| MW | < 0.0001 | 0.6059 |

| C | MW1 | MW2 |
|---|---|---|
| MW1 | 0.6455 | 0.6364 |
| MW2 | < 0.0001 | 0.5441 |

Figure 2. Similarity dendrograms and results of MRPP analyses comparing naturally occurring wetlands (NOWs) and mitigation wetlands (MWs) (dendrogram A, dashed line), NOW species assemblages defined by TWINSPAN (dendrogram B), and MW species assemblages defined by TWINSPAN (dendrogram C). The vertical node of each dendrogram is plotted at the overall mean between-group Sorensen Distance ($\bar{B}$) (Magurran 1988), and the branches representing each group end at the mean within-group Sorensen Distance ($\bar{W}_i$, $i$ = NOW or MW assemblage). The height of the node is based on plotting convenience and has no mathematical meaning. Diagonals of the matrices are $\bar{W}_i$ values. For dendrogram B, values above diagonals (dark gray shading) are the mean between-group distances for pairs of groups ($\bar{B}_{jk}$, $j$ = columns; $k$ = rows) and for dendrograms A and C they equal the overall $\bar{B}$. Values below diagonals (light gray shading) for dendrograms A and C are p-values for the overall MRPP, and for dendrogram B are the p-values for MRPP pairwise comparisons. Number of sites: NOW1, n = 15; NOW2, n = 15; NOW3, n = 15; MW1, n = 21; MW2, n = 30.

erogeneity, with only about 28% overlap in species between site pairs.

TWINSPAN yielded three clusters (NOW1, NOW2, and NOW3) for NOW sites and two clusters (MW1 and MW2) for MW sites. These groupings were based on the first two TWINSPAN divisions for NOWs ($\lambda_1$ = 0.24, $\lambda_2$ = 0.21) and on the first division for the MW analysis ($\lambda$ = 0.14). An MRPP analysis evaluating the NOW groups indicated that they had significantly different floristic compositions (Figure 2B). The overall $\bar{B}$ indicates about 25% overlap of species between site pairs for the three NOW assemblages, whereas sites pairs within the same group are more similar to one another. NOW2 was the most homogenous of the three groups, with approximately 40% ($\bar{W}_{NOW2}$ = 0.5984) of its species shared among site pairs. The NOW2 and NOW3 groups share about 34% ($\bar{B}_{NOW2, NOW3}$ = 0.6614) of their species but share only 22 and 19% of their species, respectively, with NOW1. The two MW assemblages were also significantly different ($p < 0.0001$) from one another (Figure 2C), having about 36% of their species in common. MW2,

| | NOW1 | NOW2 | NOW3 | MW1 | MW2 |
|---|---|---|---|---|---|
| NOW1 | 0.7221 | 0.7620 | 0.6283 | 0.7716 | 0.7859 |
| NOW2 | < 0.0001 | 0.5984 | 0.6614 | 0.6966 | 0.6201 |
| NOW3 | < 0.0001 | < 0.0001 | 0.6283 | 0.6780 | 0.6153 |
| MW1 | < 0.0001 | < 0.0001 | <0.0001 | 0.6455 | 0.6354 |
| MW2 | < 0.0001 | < 0.0001 | <0.0001 | < 0.0001 | 0.5441 |

(Bonferoni corrected significance value = 0.005)

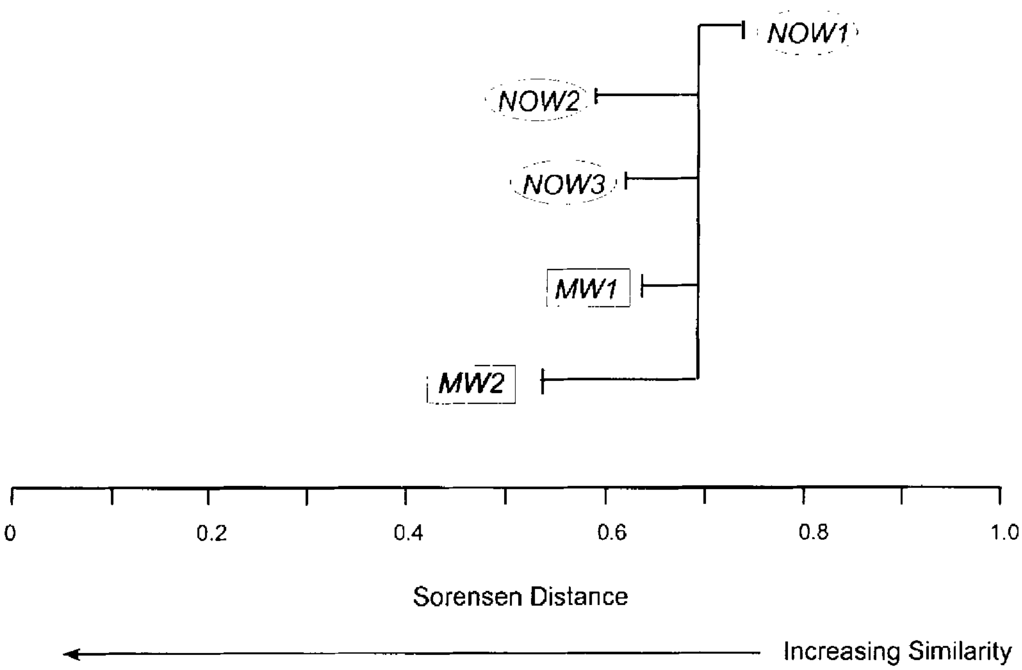
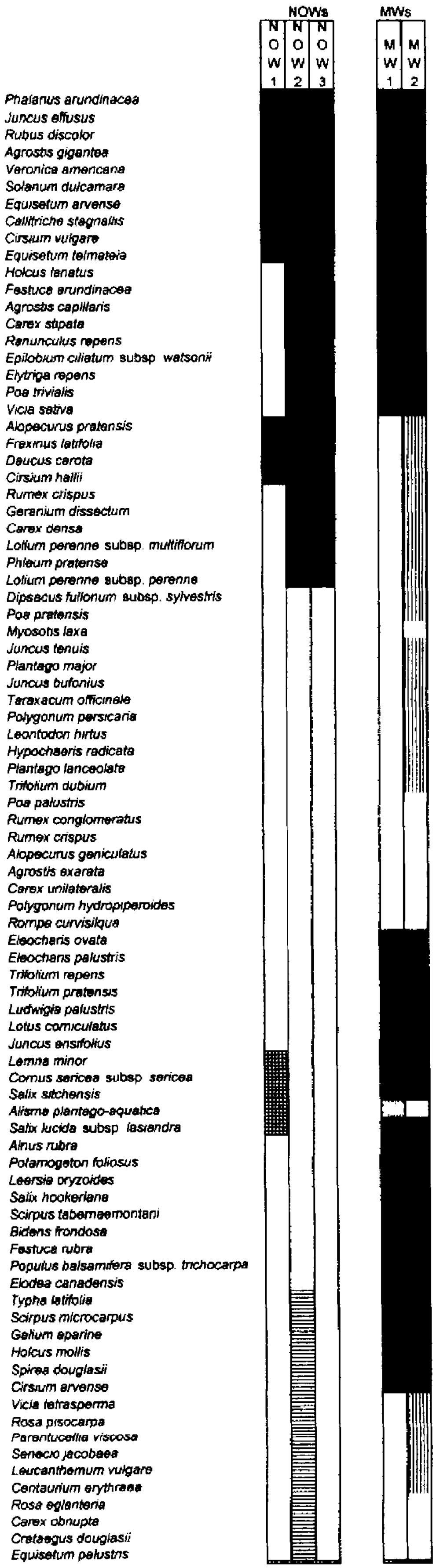



Figure 3. Similarity dendrograms and results of MRPP analyses comparing all assemblages, naturally occurring wetlands (NOW1, NOW2, NOW3), and mitigation wetlands (MW1, MW2) together. The vertical node of the dendrogram is plotted at the overall mean between-group Sorensen Distance ($\bar{B}$) (Magurran 1988), and the branches representing each group end at the mean within-group Sorensen Distance ($W_i$, $i$ = NOW or MW assemblage). The height of the node is based on plotting convenience and has no mathematical meaning. Diagonals of the matrices are $\bar{W}_i$ values. Values above diagonals (dark gray shading) are the mean between-group distances for pairs of groups ($\bar{B}_{jk}$, $j$ = columns; $k$ = rows). Values below diagonals (light gray shading) are the p-values for MRPP pairwise comparisons. Number of sites: NOW1, n = 15; NOW2, n = 15; NOW3, n = 15; MW1, n = 21; MW2, n = 30.

with 46 % ($\bar{W}_{MW2}$ = 0.5441) species shared between site pairs, had greater between-site homogeneity than MW1 (35% shared species, $\bar{W}_{MW2}$ = 0.6455). Finally, MRPP comparisons of all assemblages, both NOW and MW groups together (Figure 3), showed significantly different floristic composition between all five assemblages ($p < 0.0001$ for all pairwise comparisons, Bonferroni corrected significance value = 0.005).

Our analyses indicate that the five TWINSPAN groups shared a suite of widespread species but were characterized by different sets of species that occur preferentially in each group of sites (Figure 4). The suite of non-preferential species that is common across all assemblages is, not surprisingly, dominated by invasive/introduced taxa and by competitive or widespread native plants (FDPEM-Portland 1999). It also strongly corresponds to the species that are most common in the study wetlands (Table 2). In addition to these non-preferential species, NOW1 sites are characterized by preferential occurrence of obligate aquatic species (*Alisma plantago-aquatica* and *Lemna minor*) and facultative wetland shrubs (*Cornus sericea* ssp. *sericea* and *Salix* spp.) (Figure 4). The NOW2 and NOW3 groups had several species in common, in addition to those that were ubiquitous across all assemblages, including a native sedge (*Carex densa*), introduced seed crop or pasture grasses (*Lolium perenne* and *Phleum pratense*), and introduced forbs (*Rumex crispus* and *Geranium dissectum*).

Sites with the NOW2 species assemblage were char-




acterized by the frequent occurrence of tall, obligate, native species (*Scirpus microcarpus* and *Typha latifolia*) with clonal growth habits. NOW2 sites also often had scattered occurrences of native (*Crataegus douglasii, Rosa pisocarpa,* and *Spiraea douglasii*) and introduced (*R. eglanteria*) facultative or facultative-wetland shrubs. The most common introduced species that are preferential to this assemblage include the grass *Holcus mollis,* the annual legume *Vicia tetrasperma,* and the clonally spreading *Cirsium arvense.*

The NOW3 group was typified by the presence of native rushes (*Juncus bufonius, J. tenuis,* and *J. ensifolius*), spikerushes (*Eleocharis ovata* and *E. palustris*), grasses (*Alopecurus geniculatus* and *Agrostis exarata*), and a sedge (*Carex unilateralis*). These species ranged in wetland indicator status from facultative wetland to obligate. In addition, the native obligate forbs *Ludwigia palustris, Myosotis laxa,* and *Rorripa curvisilqua* frequently occurred on these sites. Common introduced taxa included the grass *Poa palustris* and 12 fibrous or tap-rooted perennial forbs that are often found in agricultural settings. Among these were three dandelion-like composites (*Hypochaeris radicata, Leontodon hirtus,* and *Taraxacum officinale*) two plantain species (*Plantago major* and *P. lanceolata*), two smartweed species (*Polygonum persicaria* and *P. hydropiperoides*), one dock species (*Rumex conglomeratus*), and four legume species (*Trifolium dubium, T. pratense, T. repens,* and *Lotus corniculatus*).

The two MW assemblages share the standard suite of introduced, non-preferential species common across all assemblages; however, they also share a number of native species that are preferential to individual NOW assemblages. For example, *Eleocharis ovata, E. palustris, Juncus ensifolius,* and *Ludwigia palustris* were

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Figure 4. Results of TWINSPAN analyses identifying species assemblages. Note that separate analyses were run for naturally occurring wetlands (NOWs) and mitigation wetlands (MWs). Taxa selected as pseudospecies by the TWINSPAN algorithm are listed on the left side of the diagram. Species identified by TWINSPAN as preferential (patterned shading) and non-preferential (black shading) for each NOW and each MW assemblage are indicated within columns. Note that non-preferential species are common across more than one NOW or MW assemblage. Further, many of the non-preferential species are common to both NOW and MW assemblages. Species occupying unshaded areas within a given assemblage occurred at low frequencies and were considered neither preferential nor non-preferential by TWINSPAN for that assemblage. Taxa are ordered roughly in terms of frequency of occurrence within each major block across columns. Number of sites: NOW1, n = 15; NOW2, n = 15; NOW3, n = 15; MW1, n = 21; MW2, n = 30.

| | UT | LT | W | C |
|---|---|---|---|---|
| UT | 0.6597 | | | |
| LT | 0.0108 | 0.6339 | | |
| W | 0.1944 | 0.3896 | 0.5744 | |
| C | ≤ 0.0001 | ≤ 0.0001 | 0.1645 | 0.7041 |

(Bonferoni corrected significance value= 0.008)

| | UND | RES | AG | CIT |
|---|---|---|---|---|
| UND | 0.7111 | | | |
| RES | 0.0083 | 0.6477 | | |
| AG | 0.0457 | 0.0190 | 0.6438 | |
| CIT | 0.0053 | 0.2326 | 0.1004 | 0.6201 |

(Bonferroni corrected significance value= 0.008)

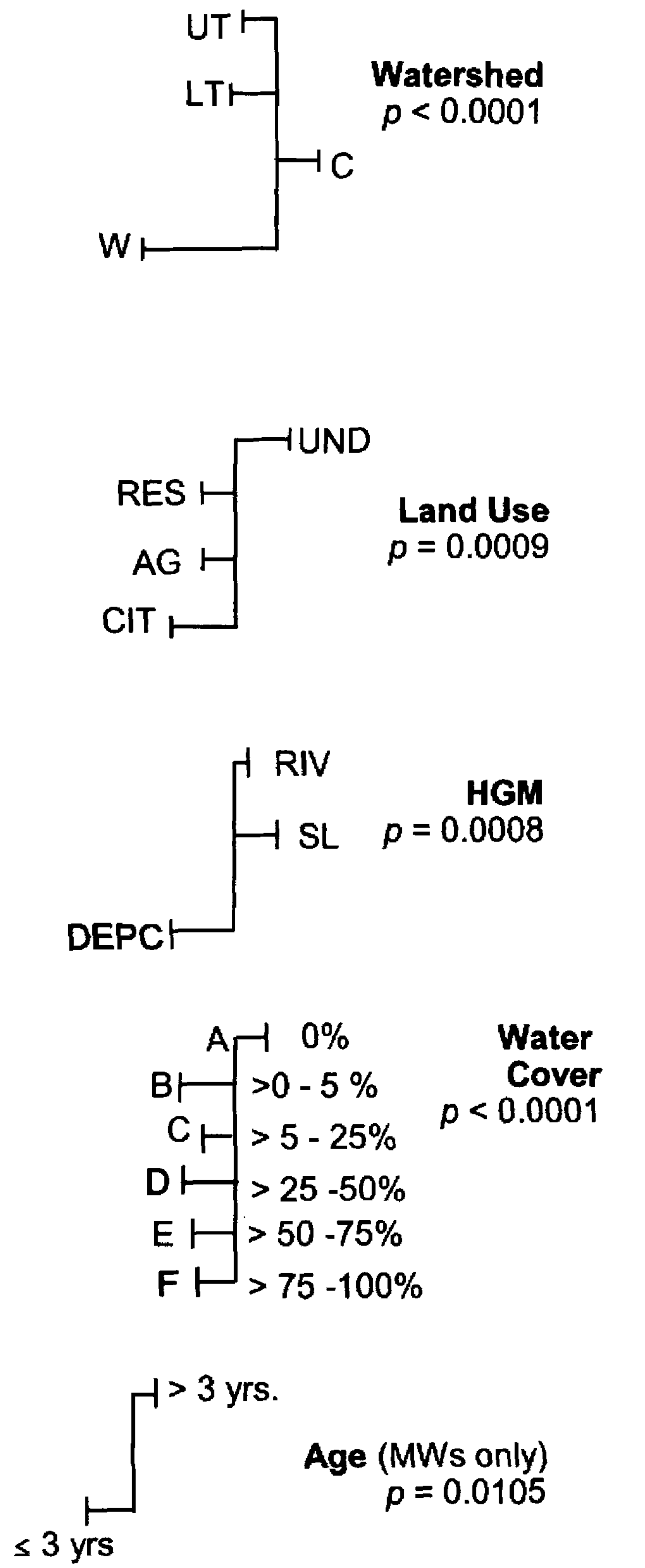
| | RIV | SL | DEPC |
|---|---|---|---|
| RIV | 0.6897 | | |
| SL | 0.5377 | 0.7101 | |
| DEPC | 0.0047 | 0.0005 | 0.6341 |

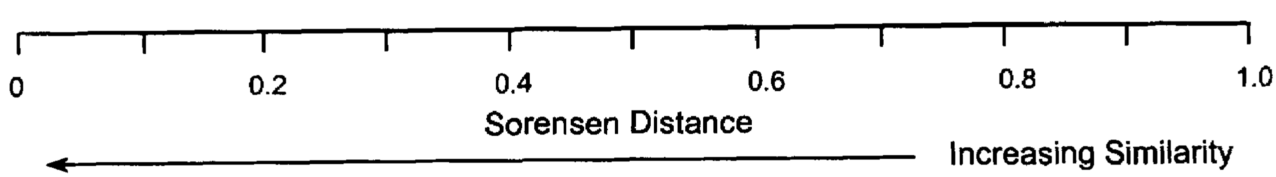
(Bonferoni corrected significance value = 0.017)

| | A | B | C | D | E | F |
|---|---|---|---|---|---|---|
| A | 0.6947 | | | | | |
| B | 0.0146 | 0.6449 | | | | |
| C | 0.0014 | 0.0789 | 0.6501 | | | |
| D | ≤ 0.0001 | 0.0008 | 0.1815 | 0.6205 | | |
| E | ≤ 0.0001 | 0.0002 | 0.0100 | 0.2125 | 0.6315 | |
| F | ≤ 0.0001 | 0.0001 | 0.0557 | 0.3567 | 0.5808 | 0.6891 |

(Bonferoni corrected significance value = 0.003)

| | ≤ 3 yrs | > 3 yrs |
|---|---|---|
| ≤ 3 yrs | 0.5621 | |
| > 3 yrs | 0.0105 | 0.6146 |



common to both MW1 and MW2 but preferential to NOW3. Similarly, there were species common across the MW assemblages that were preferential to NOW1 (*Lemna minor, Cornus sericea* ssp. *sericea, Salix lucida* ssp. *lasiandra,* and *Salix sitchensis*) or NOW2 (*Typha latifolia, Scirpus microcarpus, Galium aparine,* and *Spiraea douglasii*). However, along with species that occur across multiple NOW assemblages, an additional series of native species (Figure 4) was found primarily on MWs, including *Bidens frondosa, Leersia oryzoides, Potamogeton foliosus, Salix hookeriana,* and *Scirpus tabernaemontani.*

Differences between MW1 and MW2 were based primarily on the accession of a series of introduced species on MW2 sites (Figure 4). Due to the influx of introduced species, MW2 averages about 11 more species per site than MW1. The invasive, tall perennial *Dipsacus fullonum* ssp. *sylvestris* and the perennial grass *Poa pratensis* are preferential only to MW2. Other introduced species in this group are also common across both the NOW2 and NOW3 species assemblages (*Alopecurus pratensis, Daucus carota, Rumex crispus, Geranium dissectum, Lolium perenne,* and *Phleum pratense*). Others are preferential on MW2 sites and to either NOW2 (*Vicia tetrasperma, Parentucellia viscosa, Senecio jacobaea, Leucanthemum vulgare,* and *Centaurium erythraea*) or NOW3 (*Hypochaeris radicata, Leontodon hirtus, Plantago lanceolata, P. major, Polygonum persicaria, Taraxacum officinale,* and *Trifolium dubium*).

## Relationships of Environmental Variables to Floristic Composition

MRPP analyses for all wetlands showed that watershed, land-use, HGM class, percent cover of water, and MW age were significantly related to the floristic composition of the study wetlands (Figure 5). In the overall test, watershed was significantly related to floristic composition, while the pairwise comparisons indicated that only the Columbia and Tualatin watersheds were significantly different. For land-use, the pairwise comparisons indicated that UND was floristically different than RES and CIT. The overall MRPP test for HGM classes was significant ($p < 0.0008$), however, pairwise comparisons showed no significant differences in floristic composition based on presence/absence among the four depressional classes (See Table 1 for definitions). Consequently, these classes were grouped into a combined depressional category (DEPC) and another MRPP test was applied using riverine (RIV), slope (SL), and DEPC classes (Figure 5). The overall and pairwise comparisons indicated that DEPC was significantly different from either the RIV or SL classes, consistent with the fact that mean percent cover of water present on a site during the growing season was significantly greater (ANOVA, $F = 32.80$ at 1 and 88 df, $p = 0.0001$) for MWs (52%) than NOWs (21%), reflecting the preponderance of MWs in the depressional HGM classes. Furthermore, percent cover of water showed a strong relationship to species presence or absence in the overall MRPP test, with significant differences among the pairwise comparisons indicating a shift in floristic composition occurred within the water cover class that ranged from greater than 5% to 25% (Figure 5). Age since time of construction on MW sites also showed significant differences in floristic composition; sites less than 3 years old differed from those more than 3 years old (Figure 5).

Using the MRPP results for guidance, categories for some environmental variables were combined for use in CCA. The watershed variable was aggregated into two categories, Columbia and Tualatin/Willamette (T/W), where the Upper and Lower Tualatin and the Willamette watersheds were combined to form one category. Depending on the CCA (e.g., NOW or MW), land-use was input using either the original four classes or using UND and a combined category for developed land-uses (DEV) that incorporated RES, AG,

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Figure 5. Similarity dendrograms and results of MRPP analyses comparing floristic composition for each environmental variable for overall tests (p-value provided next to variable label) and for pairwise comparisons between groups defined by variable categories (p-values provided in matrices). Watershed: UT—upper Tualatin ($n = 37$), LT—lower Tualatin ($n = 36$), C—Columbia ($n = 19$), W—Willamette ($n = 4$). Land-use: UND—undeveloped ($n = 39$), RES—residential ($n = 17$), AG—agricultural ($n = 12$), CIT—commercial/industrial/transportation corridor ($n = 28$). HGM: RIV—riverine ($n = 31$), SL—slope ($n = 9$), DEPC—depressional HGM classes combined ($n = 54$). Water Cover—cover classes for percent of site covered with water: A ($n = 14$), B ($n = 11$), C ($n = 16$), D ($n = 16$), E ($n = 25$), F ($n = 14$). Age—age of MWs since construction: $\leq$ 3 years ($n = 14$), $>$ 3 years ($n = 37$). The node of each dendrogram is plotted at the overall mean between-group Sorensen Distance ($\bar{B}$) (Magurran 1988), and the branches representing each group in the dendrogram end at the mean within-group Sorensen Distance ($\bar{W}_i$, $i$ = NOW or MW assemblage). The height of the node is based on plotting convenience and has no mathematical meaning. Diagonals of the matrices are $\bar{W}_i$ values, and off-diagonals (light gray shading) are p-values for MRPP pairwise comparisons.

and CIT. The final environmental data matrix for CCA was composed of the continuous variables, percent cover of water and age of MWs, and the nominal variables, watershed, HGM class, and land-use. Watershed was not used in the NOW CCA because of an interaction with HGM or land-use classes that resulted in an uninterpretable biplot. The two lacustrine-fringe wetlands behaved as strong outliers in the NOW CCA and were dropped from that analysis. The ordination of the NOW CCA was plotted using axes 1 and 3 because axis 2 ($\lambda$ = 0.131) and axis 3 ($\lambda$ = 0.126) had similar eigenvalues and the use of axis 3 resulted in a more informative biplot. Age applied only to MW sites, so it was used only in the MW CCA.

The primary gradient described by the NOW CCA was related to moisture, while the secondary gradient was related to land-use (Figure 6, Table 4). Axis 1 describes a strong relationship between percent cover of water and HGM class, whereas axis 3 describes land-use. Sites representing the three species assemblages identified by TWINSPAN separate into fairly distinct groups along these two axes. Sites in the NOW1 species assemblage tended to have greater percent cover of water ($\bar{x}$ = 37% ± 36% SD) than sites in the NOW3 assemblage ($\bar{x}$ = 17% ± 24% SD), which had greater water cover than sites in the NOW2 assemblage ($\bar{x}$ = 5% ± 7% SD). Sites in the NOW1 assemblage were most often surrounded by undeveloped land-use. More than half of the NOW3 sites were surrounded by AG land-use, with the remaining sites surrounded by either UND or CIT. Wetlands with the NOW2 assemblage were predominantly associated with RES and UND land-uses.

For MWs, the first CCA axis described differences in the species distribution related to watershed location and surrounding land-use, while axis 2 described gradients related to percent cover of water and MW age (Figure 7, Table 4). The MW1 assemblage was represented by sites located in both the Columbia and Tualatin/Willamette watersheds, while none of the sites characterized by the MW2 assemblage occurred along the Columbia. The UND and DEV vectors described an urbanization gradient where 61% of the MW1 sites were associated with UND land-use and 73% of the MW2 sites were surrounded by DEV land. Although age did not clearly separate MW1 and MW2 assemblages, the MW1 sites tended to be younger (33%, > 3 years) than MW2 sites (73%, ≥3 years). Percent cover of water was also strongly related to the second axis. Sites within both assemblages were distributed along the length of the gradient, suggesting that percent cover of water is related to variability in floristic composition within each assemblage rather than to differences between the two. Most MWs (44 out of 51 sites) are depressions in various settings, so while

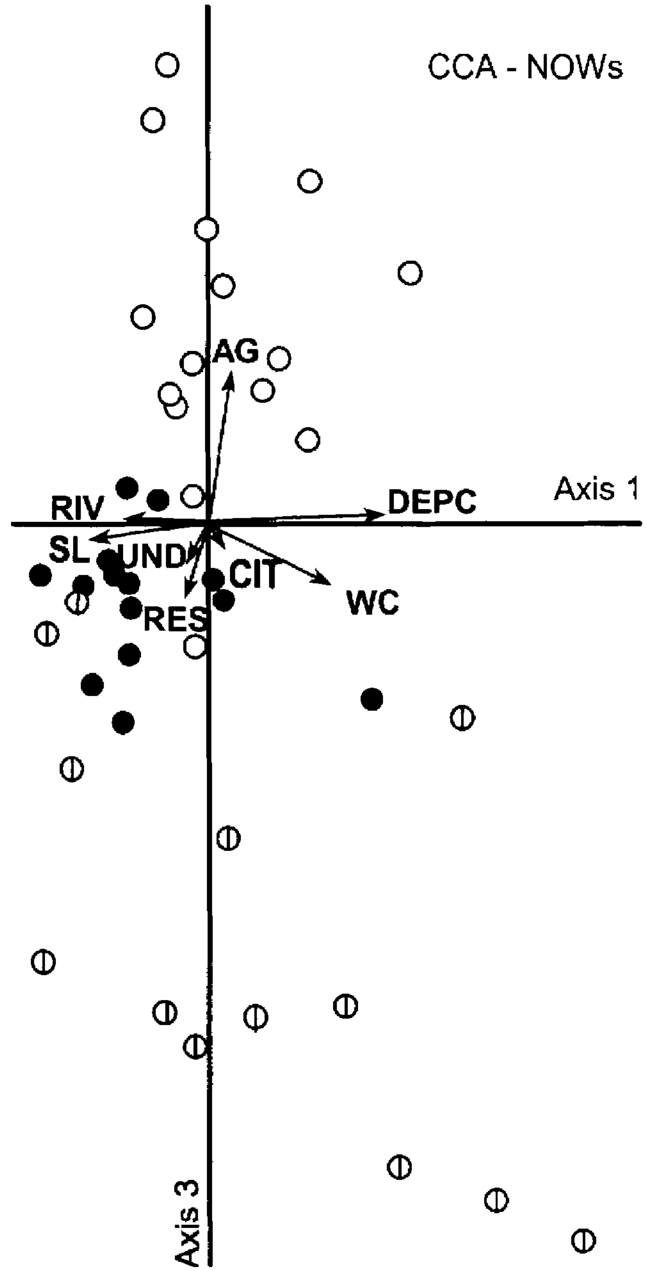


Figure 6. CCA biplot for naturally occurring wetlands (NOWs) showing the distribution of sites representing different species assemblages Ⓘ NOW1, ● = NOW2, ○ = NOW3) in relation to environmental variables. Environmental variables are represented by vectors based on biplot scores and include percent cover of water (WC), HGM classes (DEPC = combined depressional classes, SL = slope, RIV = riverine), and land-use categories (UND = undeveloped, RES = residential, AG = agricultural, and CIT = commercial/industrial/transportation corridor). See Figure 4 for details of species composition.

Table 4. Intraset correlations of environmental variables, eigenvalues (λ), and the cumulative percent of the species variance explained by the two canonical axes presented for each CCA. Important CCA axes were identified using eigenvalues, the percent of the variance in the species data explained by each axis, and Monte Carlo permutation tests to identify significant axes (ter Braak 1990, Palmer 1993). Low percentages (<10%) for the explained variance in the species data were expected as an inherent feature of data with strong gradients and a presence/absence component (ter Braak and Verdonschot 1995). P-values from Monte Carlo permutation tests for each eigenvalue are presented and were based on the null hypothesis that the species and environmental data matrices were not related. — Indicates variable not included in analysis.

| | Naturally Occurring Wetlands (n = 43) | | Mitigation Wetlands (n = 51) | |
|---|---|---|---|---|
| Variable | Axis 1 | Axis 3 | Axis 1 | Axis 2 |
| Percent Cover of Water (WC) | 0.535 | −0.330 | −0.050 | −0.609 |
| Watershed | | | | |
| Columbia (C) | — | — | −0.921 | 0.252 |
| Tualatin/Willamette (T/W) | — | — | 0.921 | −0.252 |
| Land-use | | | | |
| Undeveloped (UND) | −0.075 | −0.208 | −0.671 | −0.435 |
| Developed (DEV) | — | — | 0.671 | 0.435 |
| Residential (RES) | −0.096 | −0.357 | — | — |
| Agricultural (AG) | 0.062 | 0.680 | — | — |
| Commercial/industrial/ transportation corridor (CIT) | 0.045 | −0.122 | — | — |
| HGM class | | | | |
| Combined Depressional Classes (DEPC) | 0.914 | 0.008 | 0.089 | 0.046 |
| Slope (SL) | −0.514 | −0.041 | 0.052 | −0.055 |
| Riverine (RIV) | −0.387 | 0.025 | −0.151 | 0.125 |
| Lacustrine-fringe (LAC) | — | — | — | — |
| Age of MWs (Age) | — | — | 0.161 | 0.695 |
| CCA λ | 0.348 | 0.126 | 0.155 | 0.086 |
| % Cumulative Species Variance | 9.2 | 12.5 | 6.0 | 9.3 |
| Monte Carlo Test p-value | 0.09 | 0.04 | 0.04 | 0.05 |

HGM class separates NOWs from MWs, it does little to distinguish the MW assemblages.

## DISCUSSION

### Influence of Urban Environment on Floristic Condition

Despite relatively high species richness, the wetlands evaluated in the Portland metropolitan area, both NOWs and MWs, are floristically degraded, with over half of the observed species being introduced. Many of these introduced species (FDPEM-Portland 1999) are common in wetlands and uplands elsewhere in the Pacific Northwest (e.g., Azous 1991, Wilson et al.1995) and in other areas of North America (U.S. Congress, Office of Technology Assessment 1993). Further, the nine introduced species that occur on the majority of study wetlands are strong competitors that can become vegetation dominants or form monocultures, effectively excluding native species and potentially compromising the maintenance of native biodiversity. *Phalaris arundinacea*, the most frequent species, is a highly competitive (Gaudet and Keddy 1995), clonal dominant (Boutin and Keddy 1993) that aggressively invades native wetland plant communities in the Pacific Northwest (Taylor 1990, Naglich 1994, Guard 1995, Houck 1996). *Phalaris arundinacea* is considered to have native genotypes in the region; however, much of its current extent on the landscape is believed to be represented by rapidly spreading cultivars introduced for forage and erosion control (Guard 1995, Naglich 1994). It is a turf-forming grass that propagates effectively from sod, stem pieces, or seed (Marten 1985, Naglich 1994); forms monocultures in well-drained to inundated soil; tolerates seasonal fluctuations in water depth (Weinmann et al. 1984, Marten 1985, Rice and Pinkerton 1993, Taylor 1993, Galatowitsch and van der Valk 1996); and may increase in abundance with urbanization and storm water run-off (Cooke and Azous 1993). Five of the other most com-

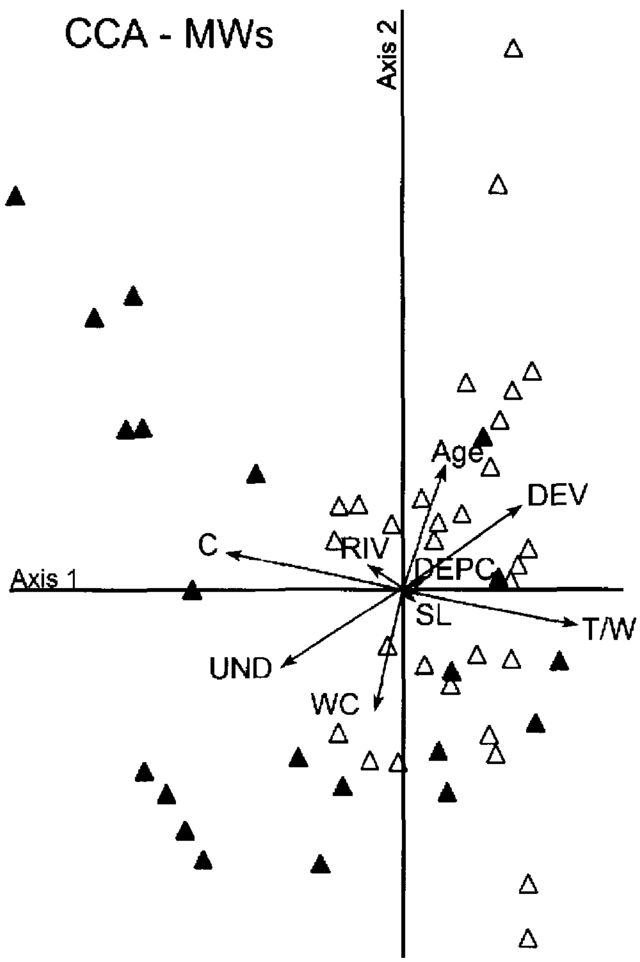


Figure 7. CCA biplot for mitigation wetlands (MWs) showing the distribution of sites representing different species assemblages (MW1 = ▲, MW2 = △) in relation to environmental variables. Environmental variables are represented by vectors based on biplot scores and include percent cover of water (WC), HGM classes (DEPC = combined depressional classes, SL = slope, RIV = riverine), land-use (UND = undeveloped, DEV = residential, agricultural, and commercial/industrial/transportation corridor), watershed (T/W = Tualatin and Willamette, C = Columbia), and age. See Figure 4 for details of species composition.

mon introduced species are invasive perennial grasses (*Agrostis capillaris, A. gigantea, Alopecurus pratensis, Festuca arundinacea,* and *Holcus lanatus*) that are widely used in agriculture (Marten 1985). All produce tall or medium closed canopies; spread rapidly by extension of rhizomes, creeping stolons, or tillering; and form near monocultures or, if tufted, grow in dense clusters (Hitchcock et al. 1969, Taylor 1990, Guard 1995, Whitson et al. 1996). In contrast, only five native species occur on more than half of the study wetlands, and of these, *Juncus effusus* and *Typha latifolia* were often observed as patch dominants within individual wetlands.

The dilution of native species assemblages by introduced species is exacerbated by intensive land-use in the area adjacent to a wetland. Although the mean number of native species per site is similar among land-use settings, the number of introduced and invasive/introduced species per site increases significantly with more intensive land-use. In particular, wetland plant communities surrounded by agricultural or commercial/industrial land-use are at greater risk for invasion by introduced or invasive/introduced species than wetlands that are contiguous with undeveloped land. Similar increases in introduced species related to land-use and disturbance have been observed in wetlands elsewhere in the world (Puget Sound Lowlands of Washington—Cooke and Azous 1993, Houck 1996; New Jersey Pinelands—Ehrenfeld and Schneider 1991, 1993; New South Wales, Australia—McIntyre et al. 1988).

Nevertheless, wetlands with severe floristic degradation may still be important reservoirs of seeds or other propagules for local populations of native wetland species. In this study, many native species (n = 131) were observed on 5 or fewer wetlands (FDPEM-Portland 1999), and continued urbanization may place some of them in jeopardy of local extirpation due to competition from introduced weeds or conversion of wetland habitat to other uses. Also, the naturally occurring wetlands represent disturbed remnants of an increasingly rare wetland prairie ecosystem that historically was extensive in the Willamette Valley (Davis 1995, Noss et al. 1995, Christensen et al. 1996) or of marsh communities that were previously common in floodplain locations (Guard 1995). Thus, NOWs with high native species richness or relatively intact assemblages may be critical for conserving or restoring native biodiversity, by functioning as refugia for native wetland species and local genotypes, and for preserving fragments of endangered or rare ecosystems.

## Differences and Similarities Between NOWs and MWs

As currently built, Portland area MWs have led to the replication of wetland types different from existing NOWs and the wet meadows or marshes historically common in the region. Floristic composition was significantly different between NOWs and MWs, and differences were related to the fundamentally different hydrogeomorphic conditions. MWs had greater mean percent cover of water during the growing season than NOWs and were primarily depressional HGM classes that do not occur naturally in the landscape compared to the primarily riverine and slope classes observed for NOWs (Gwin et al. 1999). Intensive hydrologic monitoring on 45 of our study wetlands from 1993 to 1996 showed that MWs have more extensive and persistent flooding with less annual fluctuation in water levels than NOWs (Shaffer et al. 1999). The uniformity in environmental conditions in MWs is reflected in the restricted spatial extent of vegetation compared to NOWs. MWs in our study area often have large perennially flooded areas with expanses of open water (Gwin et al. 1999), bordered by a narrow vegetated area, a pattern frequently observed elsewhere in the country (e.g., Confer and Niering 1992, Kentula et al. 1992b, Bedford 1996). On NOWs, we observed that emergent or wet meadow vegetation was generally distributed continuously across the entire site, particularly for slope and riverine HGM classes, and any standing water present is typically shallow and not ponded (Shaffer et al. 1999).

Even with important differences in hydrogeomorphic conditions, floristic composition, and spatial distribution of vegetation, the five species assemblages of NOWs and MWs shared a core group of widespread invasive/introduced species and competitive native species (Figure 3, Table 2, FDPEM-Portland 1999). The existence of this shared group is likely related to the frequent construction of MWs within existing NOWs (Gwin et al. 1999) and the probable inheritance by MWs of species from their parent NOWs. Despite the similarities in floristic composition, 3 NOW and 2 MW species assemblages were distinguished based on the addition of diagnostic suites of native and introduced taxa to the core group. Further, the primary environmental gradients along which MW and NOW assemblages are distributed are different. The two MW assemblages differ from one another principally in the addition of a series of introduced species in MW2 compared to MW1. This influx of weedy species may be related in part to MW age and to the time required for successful invasion and establishment on site. Younger sites ($\leq$ 3 years) are frequently represented by the MW1 assemblage and tend to have fewer introduced species than the older sites (4–11 years) commonly represented by the MW2 assemblage. The older and weedier MW2 assemblage was more frequently associated with the more urbanized Tualatin/Willamette watersheds, whereas sites in the MW1 assemblage were associated with the less urbanized Columbia watershed and were often surrounded by undeveloped land. Thus, the floristic composition of MWs seems to vary mainly in relation to the level of development in the surrounding area and to the age of the wetland. In contrast, the three NOW assemblages are characterized by distinguishing suites of native and introduced species, and the assemblages are distributed across a moisture gradient (from very wet to seasonally dry sites) and are influenced secondarily by the surrounding land-use.

Finally, although MWs have lower between-site floristic heterogeneity than NOWs, suggesting a potential simplification in diversity of species assemblages, they also have greater species richness, suggesting that individual wetlands may be more complex floristically. The ecological significance of greater native species richness and the apparent increased frequency of common obligate and facultative wetland species in MWs (e.g., *Typha latifolia, Eleocharis* sp., *Juncus* sp., *Scirpus* sp., and *Salix* sp.) compared to NOWs is difficult to assess. The potential benefit to native biodiversity of greater native richness on MWs is confounded by the concomitant increase in the occurrence of invasive species, the limited spatial distribution of vegetation on MWs, the apparent influx of introduced species that may be occurring over time on the MWs, and by shifts in the relative abundances of wetland types across the region. Further, the contiguous location of many MWs with NOWs and the greater frequency of introduced species on MWs may provide new dispersal routes for invasive species detrimental to native plant assemblages. MWs may also contribute to the influx of species not previously observed on NOWs. For example, among the introduced species that were found only on MWs, there were three invasive species (*Myriophyllum spicatum, Hedera helix,* and *Typha angustifolia*) and nine shrubs or trees of likely horticultural origin (FDPEM-Portland 1999). We plan to address some of these issues in ongoing research aimed at identifying specific topographic and hydrologic conditions associated with native species richness, abundance, and temporal persistence.

In summary, urbanization in the Portland metropolitan area is resulting in cumulative degradation of the floristic condition of wetlands, and current wetland management practices are resulting in a cumulative shift in wetland types from wet meadows and marshes to ponds. The combined influences of land-use changes, hydrologic modification, and wetland management have altered native plant diversity in northern Willamette Valley wetlands through 1) dilution of the native flora with introduced species and 2) modification and replacement of naturally occurring wetlands with mitigation wetlands having different species complements and hydrogeomorphic characteristics than those in naturally occurring wetlands.

## ACKNOWLEDGMENTS

We are indebted to Stephanie Gwin, Paul Shaffer, Charlie Halpern, Kathryn Freemark, Thom Whittier, Robert Meinke, Bill Niering, and two anonymous referees for thoughtful reviews of earlier drafts of this manuscript. We thank John Van Sickle for introducing us to the use of mean similarity dendrograms. Special thanks go to the landowners who allowed us access to the wetland study sites and to Bill Becker, Neil Maine, and Portland State University for providing us with the opportunity to recruit and train educators as field crew members. We gratefully recognize the dedication in the field and the high quality of data collected by the 23 elementary and secondary teachers who made up our field crews, particularly those who served as botanists and recorders—Joe Blowers, Gail Cape, John Colvin, David Ellenberg, Maureen Kelly, John McGinty, Eric Olsen, Gail Peterson, Mary Pfauth, Russ Roseberry, Janice Thompson, and Gordon Whitehead. Sherry Spencer provided logistical and botanical support to the field crews; JoEllen Honea, Stephanie Gwin, and Cindy Holland served as field crew leaders. We thank Robert Gibson for careful data management and Ty Hildreth for data entry. In addition, Miriam Pendergraft and Craig McFarlane provided helpful editorial and quality-assurance review, respectively. The research described in this paper was funded by the U. S. Environmental Protection Agency at the USEPA National Health and Environmental Effects Laboratory, Western Ecology Division, in Corvallis, Oregon, through Contract No. 68-C8-0006 to 68-C6-0005. Suzanne Pierson, of OAO Corporation, produced Figure 1, under EPA contract 68-W5-0065. This document has been subject to the Agency's peer and administrative review and approved for publication. Mention of trade names or commercial products do not constitute endorsement or recommendation for use.

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Manuscript received 1 June 1998; revisions received 1 March 1999, 20 May 1999, and 2 June 1999; accepted 4 June 1999.