Scaling considerations of mesocosm wetlands in simulating full-scale wetlands

Changwoo Ahn and William J. Mitsch

Environmental Science Graduate Program and School of Natural Resources
The Ohio State University

Abstract

To explore the effects of experimental scale on ecological functions in wetlands, flow-through mesocosm wetlands (1 m²) were compared over the first two growing seasons to a full-scale, created, flow-through wetland (10,000 m²) over four early growing seasons. Hydrology was generally similar. Mean hydraulic loading rates (HLR) were 7.8 cm day⁻¹ for full-scale wetland (excluding an extensive flooding year of 1995) and 6.3 cm day⁻¹ for mesocosms; mean hydraulic retention time (HRT) was 2.1 days for full-scale wetland and 1.7 days for mesocosms. Temperature decreased slightly from inflow to outflow in mesocosms while it increased in the full-scale wetland because of differences in macrophyte development. Conductivity of water in mesocosms showed no significant changes from inflow to outflow while it decreased significantly in the full-scale wetland. Phosphorus was retained effectively in the full-scale wetland for 3 of 4 years and was retained in the mesocosms for the first year. However, phosphorus was exported in the second year in the mesocosms as dissolved oxygen and redox potential dropped significantly. Higher macrophyte peak biomass occurred in mesocosm wetlands (~ 1,200 g m⁻²) after two years compared to the full-scale wetland (~ 800 g m⁻²) after four years. Plants colonized fully in mesocosms over two growing seasons not allowing any open space in the surface water. The more extensive shading of the water column in mesocosms led to decreases in water temperature, less surface turbulence and therefore less oxygen diffusion into water, and less water column productivity. These may have stimulated reduced conditions in mesocosm sediments more rapidly than in the full-scale wetland, thereby causing the release of phosphorus. Scale of experiments must be considered carefully before the results from wetland mesocosm studies are generalized to full-scale wetlands.

Introduction

Mesocosms have long been considered useful research tools for ecological studies of aquatic and terrestrial ecosystems (Grice and Reeve, 1982; Odum, 1984; Lalli, 1990; Adey and Loveland, 1991; Beyers and Odum, 1993; Kangas and Adey, 1996). They have been used in commercial scale applications, such as in wastewater treatment or food production of ecological engineering (Kangas and Adey, 1996) and in ecosystem restoration (Callaway et al., 1997).

Use of mesocosms, particularly in wetland science, has been common over the last two decades in studies of the fate and effect of pollutants, biogeochemical cycles and the effects of nutrients on ecosystem dynamics. Many applications of these mesocosms have been well documented (Johnson, 1986; Day et al., 1989; Wieder et al., 1990; Horne, 1991; Busnardo et al., 1992; Gale et al., 1993; de Szalay et al., 1996; Elder et al., 1997; Ahn et al., in press). Mesocosms provide a means of conducting ecosystem-level experiments under replicated, controlled, and repeatable conditions with relatively low cost (Kemp et al., 1980; Banse, 1982; Odum, 1984).

Mesocosms, however, have certain limitations (Carpenter, 1996; Schindler, 1998). A complex array of interactions found in natural ecosystems cannot always be simulated by mesocosms (Clements et al., 1988; Carpenter, 1996; Schindler, 1998). Some have criticized micro- or mesocosm approaches in ecological studies since they contain intrinsic artifacts which may confound extrapolation of results from controlled experiments to conditions in natural ecosystems (Pilson and Nixon, 1980; Carpenter, 1988; 1996; Mac Nally, 1997; Schindler, 1998; Gry et al., 1999). Therefore, decisions for ecosystem management cannot be made with confidence unless ecosystem scales are studied (Schindler, 1998) and the limitations of mesocosm studies realized.

Criticism of mesocosm scale studies has stimulated the need for whole ecosystem experiments to investigate ecological processes and functions on a large scale (Carpenter et al., 1995, Mitsch and Wilson, 1996, Mitsch et al., 1998). Ecosystem experiments on this scale are important because they include major processes not often found in smaller-scale experiments in container-held experimental systems, such as mesocosms and microcosms. However, full-scale ecosystem experiments preclude replication due to extensive land requirements and construction and monitoring costs.

The importance of scale as a determinant of the patterns and processes in natural ecosystems has been increasingly recognized in ecology over the past two decades. Attention has been paid to scaling issues in ecology since the mid-1980s (Odum, 1984; Bloesch et al., 1988; Carpenter, 1988; 1995; 1996; Levin, 1992; Schneider, 1994; Petersen et al., 1997; Fairweather and Quinn, 1998; Peterson and Parker, 1998; Petersen et al., 1999; Whittaker, 1999). It does not
seem reasonable to predict what would occur at the ecosystem level through direct extrapolation of the results obtained from small-scale experimentation. Ecological complexity is to some degree reduced or lost in microcosm or mesocosm studies depending on the size of the mesocosms being used relative to a whole-ecosystem research and on the research questions being investigated. Scale can change pathways of nutrient cycling, number of trophic levels, number of species within trophic levels, habitat types, and connectivity between habitats (Beyers and Odum, 1993). Yet the advantages of meso-scale experiment, namely low cost and replication possibilities, lead to the frequent use of these ecosystem “models”.

Few studies have specifically compared the results of similar experimental conditions conducted at vastly different scales. The primary goal of this study was to compare results from mesocosms (1 m²) with a full-scale experimental wetland (10,000 m²) in similar experimental conditions (hydrology, water chemistry of inflow) to better elucidate positive and negative aspects of using mesocosms in wetland science. Mesocosm wetlands were compared for hydrology, water quality changes and macrophyte productivity over the first two growing seasons with a full-scale, long-term created experimental wetland over its first four growing seasons.

Materials and Methods

**Full-scale wetland (10,000 m²)**

A whole-ecosystem, long-term wetland experiment was started in 1994 with two created, 10,000 m² basins constructed on the floodplain of the Olentangy River in Columbus, Ohio (Figure 1a; Mitsch et al., 1998). Olentangy River water is fed to this wetland at rates of 20 – 40 m yr⁻¹. The soil in the wetland basins was classified as Ross series, loamy mesic Cumulic Hapudoll prior to wetland construction. Although the full-scale, long-term wetland experiment began in 1994, there was no significant macrophytic vegetation cover in either wetland basin until 1995; therefore we chose the four early years (1995 through 1998) as targets of our observation for the comparison of hydrology, water quality and macrophyte productivity with the experimental mesocosm wetlands. The year of 1994 can be regarded as an acclimation period of full-scale wetland as macrophytes were introduced in May 1994. Seasonal effects were excluded from the study by comparing only growing season data (July and August). All data used for the full-scale wetland were obtained from the planted full-scale wetland (Wetland 1; bottom basin in Fig. 1a).

The experimental design, site description, and hypothesis of a full-scale ecosystem experiment at the ORWRP are summarized in Mitsch et al. (1998). Details of regional groundwater and surface hydrology are reported in Koreny et al. (1999). Water quality from the full-scale wetlands have been documented through the years since they were created and can be found in Mitsch et al. (1998), Nairn and Mitsch (2000), and Spieles and Mitsch (2000). Algal mat development in the early years is described in Wu and Mitsch (1998). Mitsch et al. (1998), Mitsch and Bouchard (1998), and Bouchard and Mitsch (1999) describe macrophyte development for the first several years.

**Mesocosm wetland (1 m²)**

Mesocosms (1 m² each) were installed starting in the spring of 1995 at the ORWRP to allow more controlled and replicated experiments with wetlands (Figure 1b). A set of ten flow-through mesocosms (= 0.8 m x 1.3 m x 0.6 m polyethylene tubs) (Figure 1b; Fig. 2) were used in this study for two growing seasons in hydrologic conditions similar with the full-scale wetland while serving as controls for another experiment (Ahn et al., in press). Mesocosms were buried in the ground to insulate roots against freezing. Each mesocosm received 10 cm of noncalcareous river pea gravel (completely covering the drain to the standpipe) overlain by 25 - 30 cm of topsoil from the site, the same kind as in the full-scale wetland (Figure 2). Soil was not compacted and some initial settling occurred. Macrophytes were planted in the mesocosms in May 1997. Three Schoenoplectus tabernaemontani (soft-stem bulrush) rhizomes, representative wetland vegetation in the full-scale basin (> 80 % of plant cover at that time), were planted into each mesocosm. The rhizomes were equally spaced lengthwise in the mesocosm, pressed just below the surface of moist soil and shallowly buried (3 cm depth). A water delivery system was constructed to the mesocosms through a series of manifolds and valves which distributed similar volumes of water pumped from the Olentangy River to each of the ten mesocosms (Figure 1b). This water was first stored in a 1600-L tank. A continuous inflow rate of 60 mL min⁻¹ (8.6 cm day⁻¹) was chosen as a target inflow to each mesocosm in the first year. Because steady flow rates at this scale were difficult to maintain, a pulse system was used to deliver a similar, per-day volume, one hour per day, in the second year of mesocosm study. A sprinkler system timer was used to program the pulse time and duration. Water levels were checked three times a week and water flow was measured with a graduated cylinder and a timer. Hydrology, as measured by water levels or water flow rates, among each of the ten mesocosms varied within 15 %. Standing water levels of about 10 cm were maintained during this comparison.

**Sampling and analysis of water quality**

Water sampling for nutrient analyses has been conducted in the full-scale wetland every week as one of the monitoring practices for the ORWRP whereas all other water quality parameters such as temperature, turbidity, dissolved oxygen, pH, conductivity, redox potential have been recorded through samplings of twice-per-day. Sampling scheme and methodology used for water quality analysis in the full-scale wetland are summarized in Nairn and Mitsch (2000) and Spieles and Mitsch (2000). We used two months’ (July and August) of nutrient and water quality data each year over a 4-year period (1995 through 1998) from the full-scale wetland for the scale comparison with mesocosm wetlands. In addition, three to five (June through October)
months’ data from each growing season were used to address the effects of flooding events in 1995 on hydraulic loading rate and phosphorus removal in the full-scale wetland. Water samples from the full-scale wetland were analyzed in the same way through the years as with mesocosm samples (see the next paragraph) with a couple of exceptions. Nutrients in water samples collected from the full-scale basin in 1995 were analyzed in the Water Quality Laboratory at Heidelberg College, Tiffin, Ohio (Nairn and Mitsch, 2000) and NO$_3$+NO$_2$ from the full-scale wetland in 1996 was measured with a Solomat 520C monitor and an Orion ion selective electrode (Spieles and Mitsch, 2000).

Mesocosm water sampling was done three times-per-week for one month over two growing seasons. A Hydrolab H20G Multiparameter Water Quality Data Probe was used to measure temperature, dissolved oxygen, pH, conductivity and redox potential through the period of experiments. The H20G was calibrated on a weekly basis during the experiments. Surface outflow samples were collected directly from the outlets of each mesocosm (Figure 2), transported to the Ecosystem Analytical Laboratory at the Ohio State University in a cooler and kept in a freezer at 4°C until analysis. One subsample was filtered through a 0.45 mm filter and placed in a freezer for later soluble reactive phosphorus (SRP) analysis. Filters were soaked for approximately 24 hr in distilled water to remove contamination. Unfiltered subsamples were preserved by acidification with 2 mL 36 N H$_2$SO$_4$ per L of sample (to pH < 2) immediately upon return to the lab. Turbidity was determined on the day of sampling on unfiltered samples with a Hach Model 18900 Ratio Turbidimeter. Analyses for total phosphorus (TP) (APHA, 1992 4500-PF), SRP (APHA, 1992 4500-PF) and nitrates (NO$_3$+NO$_2$-N) (APHA, 1992 4500-NO3E) were done on the LACHAT QuickChem IV Flow Injection Analysis (FIA) System. All samples and standards were at room temperature and were vigorously
mixed by inversion for analysis. Five prepared standards, a check standard and distilled water blank were run each time an analysis was conducted. Standards were always within 10% of the prescribed values.

### Macrophyte productivity

Macrophyte aboveground biomass productivity in the full-scale wetland was estimated as peak biomass in previous studies (Weihe and Mitsch, 1996; Mitsch and Bouchard, 1998; Bouchard and Mitsch, 1999) and multiplied by percent plant cover of the full-scale wetland basin for each corresponding year. Total biomass of the full-scale wetland both in early two years (1995, 1996) was calculated by a regression equation developed by Weihe and Mitsch (1996). Aboveground biomass of another two later years (1997, 1998) was obtained by actual field harvesting (Mitsch and Bouchard, 1998; Bouchard and Mitsch, 1999). The belowground biomass of those years was reasonably assumed to be the same as the aboveground biomass (i.e., 1:1 ratio of above- to belowground biomass; Mitsch and Bouchard, 1998).

In mesocosm experiments, total number of stems and stem lengths were investigated weekly in each mesocosm over two growing seasons to measure plant growth in 1997 and 1998. For the stem length, 20 randomly chosen stems were measured for each mesocosm with a ruler. Macrophyte biomass harvesting was carried out at the end of second-year of mesocosm measurement (September 1998); all procedures used for harvesting and biomass measurements followed the methods conducted in the full-scale wetland (Mitsch and Bouchard, 1998). Aboveground stems were cut at the soil surface and belowground roots and rhizomes were harvested. Plant samples were placed in plastic bags and weighed in the field with a hanging balance (accuracy to 40 g). Sub-samples were taken to a laboratory where both wet- and dry weight were determined to estimate dry/wet ratios. Ratios were multiplied by total wet weight of the biomass from each mesocosm to estimate each dry weight production afterward. Two regression equations were developed between plant morphometric measurements and the above- and belowground biomass harvested from mesocosms in the second year [CSL (= avg. stem length X number of stems) and biomass were regressed] to estimate the above- and belowground biomass production of the first year in the mesocosms.

\[
\begin{align*}
B_a &= 0.01655 \times X \times CSL - 134.87, \text{ n}=10, R^2 = 0.91 \quad (1) \\
B_b &= 0.0204 \times X \times CSL - 112.81, \text{ n}=10, R^2 = 0.45 \quad (2)
\end{align*}
\]

where,

- \(B_a\) = aboveground biomass, g-DW m\(^{-2}\)
- \(B_b\) = belowground biomass, g-DW m\(^{-2}\)
- CSL = cumulative stem length, cm

### Statistical analysis

Data analyses were conducted as a two-way analysis of variance using the General Linear Model (GLM) procedure in SAS (SAS Institute, 1988) with year (time) and spatial scale as main effects for all the items measured in water quality. Multivariate analysis of variation (MANOVA) was also executed to find, if any, variables closely related with nutrient retention function of wetlands being potentially changed with scale, through which we can understand the artifacts of mesocosms potentially causing any difference we may observe between the two wetlands at different spatial scales. For water quality data, averages of the parameters measured were calculated for each treatment over each growing season and then used for statistical analysis. Tukey’s multiple tests were used to test all pairwise contrasts of means for significance at \(P < 0.05\) (Steel et al., 1997). The comparison of water quality parameters between inflow and outflow was conducted via two-sample unpaired t-tests assuming unequal variance at \(P < 0.05\).

### Results

#### Hydrology/Hydraulics

Hydrologic results for the full-scale and mesocosm wetlands in the study are summarized in Table 1. General hydrology was similar between the two wetlands, with 7.8 cm day\(^{-1}\) of mean HLR for full-scale wetland excluding the flooding year of 1995 and 6.3 cm day\(^{-1}\) for mesocosms. In addition to pumping, two natural flooding events (overflow from the river) occurred on June 27th and on August 8th of 1995 in the full-scale wetland, which increased the hydraulic loading rate greatly during the growing season (Table 1) (Figure 4). Flooding events in 1995 also increased phosphorus loading rate (= 56.7 mg-P m\(^{-2}\) day\(^{-1}\)) in the full-scale wetland compared to the average value for the other 3 years (13.4 mg-P m\(^{-2}\) day\(^{-1}\)) (Table 1). But, a reasonable retention of nutrients (N, P) was observed in the growing season of 1995 regardless of the flooding events (Table 3) (Figure 4). Retention time of water ranged from 1.5 -2 days across the spatial scales compared except for the full-scale wetland in the growing season of 1996, which had a retention time of more than 3 days.

It is difficult to calculate the exact water velocity of the two wetlands due to many boundary and changing conditions. Water velocity could be roughly estimated for both types of wetlands by dividing the volumetric surface water flow per unit width (m\(^3\) m\(^{-2}\) day\(^{-1}\)) at the mid point of the distance from inflow by unit cross sectional area (water depth X unit width) of the wetlands. Channelized water flow was assumed for the calculation in both flow-through wetlands at different spatial scales. Mean water velocity was 0.54 m day\(^{-1}\) for the full-scale wetland and 0.49 m day\(^{-1}\) for the mesocosms. The full-scale wetland showed relatively slower movement of flow in 1996 (0.23 m day\(^{-1}\)) where the retention time of water was longer than the other counterparts compared.

#### Physicochemistry

All water quality parameters measured from the full-scale wetland and mesocosms are reported in Table 2 and Table 3. Temperature showed an opposite trend between the full-scale wetland and mesocosms. The full-scale wetland
showed significant increase of temperature from inflow to outflow over the 4-year period (6 % on average) while mesocosms showed a significant decrease over a 2-year period (5 % on average) (Table 2). This is attributed to fully-grown plants shading almost the whole surface water of the mesocosms (see Plant productivity below).

Turbidity decreased significantly throughout both types of wetlands overall (Table 2) probably through settling and sedimentation. Dissolved oxygen (DO) increased significantly through the full-scale wetland in two of the four years while it did not change significantly in the first year of mesocosm operation, and actually decreased by more than 50% in the second year (Table 3), resulting in no change with the two-year average (Table 2).

There was no TP retention observed in the growing season of 1997 for the full-scale wetland and actually a significant export (25%) in the second year of the mesocosms (Table 3) (Figure 3). Nitrate plus nitrite retention was significant through the years in the two different wetlands and averaged 54% for the full-scale and 65% for mesocosm wetlands (Table 3); this is a typical pattern observed in wetland systems (Gale et al., 1993; Kadlec and Knight, 1996; Mitsch et al., 2000; Mitsch and Gosselink, 2000).

**Plant productivity**

Higher plant productivity was observed in mesocosms relative to the full-scale wetland (Table 4). Estimates of above- and belowground production of similar species in natural wetlands range from 1 to 1056 g m⁻² year⁻¹ and from 87 to 2,009 g m⁻² year⁻¹, respectively (Busnardo et al., 1992). Peak biomass observed through this study fell reasonably within these ranges (Table 4). The mesocosm plants, however, were fully established by the second year in the mesocosms, covering almost the whole surface of mesocosms.

**Discussion**

We could observe a number of differences between the full-scale and mesocosm-scale wetland compared through this study. Evaluation of both scales of wetland for their functions can be done in many different categories (Table 5).

**Hydrology**

Hydrologic conditions for the two wetland scales were similar, but the retention time for the full-scale flow-through wetland might be overestimated because it was calculated based on the assumption that the entire volume of water in the wetland is involved in the flow. This is not always the case since there can be short-circuiting of

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</tr>
</thead>
<tbody>
<tr>
<td>Hydraulic loading rate (cm d⁻¹)</td>
<td>23.8</td>
<td>8.2</td>
<td>6.2</td>
<td>9.1</td>
<td>7.3</td>
<td>5.3</td>
</tr>
<tr>
<td>Mean water depth (cm)</td>
<td>44.4</td>
<td>27.9</td>
<td>10</td>
<td>14</td>
<td>10.8</td>
<td>10.2</td>
</tr>
<tr>
<td>Water volume (average, m³)</td>
<td>4,440</td>
<td>2,790</td>
<td>1,000</td>
<td>1,400</td>
<td>0.11</td>
<td>0.10</td>
</tr>
<tr>
<td>Hydraulic retention time (days)</td>
<td>1.9</td>
<td>3.4</td>
<td>1.6</td>
<td>1.6</td>
<td>1.5</td>
<td>1.9</td>
</tr>
<tr>
<td>Phosphorus loading rate (mg-P m⁻² d⁻¹)</td>
<td>56.7</td>
<td>16.2</td>
<td>9.9</td>
<td>14.0</td>
<td>10.2</td>
<td>6.7</td>
</tr>
<tr>
<td>Nitrate loading rate (mg-N m⁻² d⁻¹)</td>
<td>390</td>
<td>400</td>
<td>90</td>
<td>210</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>

a Growing season indicates two months (July and August) for full-scale wetland and one month (July or August) for mesocosms.

b Higher hydraulic loading due to flooding event (June 27th and August 8th, 1995).

c Nitrogen as NO₃ + NO₂

pH of surface outflow increased in both full-scale wetland and mesocosms probably due to photosynthetic activity in their water columns (Table 2). Conductivity in the mesocosm wetlands showed no change overall (Table 2), but an increase in the first year and a decrease in the second year (Table 3). The full-scale wetland showed significant decreases of conductivity through the years consistently from inflow to outflow (Table 2), an effect related to extensive summer calcite precipitation verified in this experimental wetland (Liptak, 2000). Redox potential of surface water flowing through both the full-scale and mesocosm-scale wetlands decreased each year, but dramatically decreased in the second year of mesocosm wetlands by more than 40% (Tables 2 and 3).

**Nutrient retention**

Both scales of wetlands showed effective nutrient retention in most growing seasons (Tables 2 and 3). Figure 3 shows that the two experimental wetlands had generally similar inflow and outflow phosphorus concentrations through the years observed. SRP was removed by 80% on average from inflow to outflow in mesocosms and the full-scale wetland (Table 2 and 3). Retention of TP in both types of wetland averaged 52% over 4 years for the full-scale and 24% over 2 years for the mesocosm wetlands (Table 2).
Table 2. Mean water quality and nutrient changes (mean ± S.E., (n)) during the growing seasons of two wetland scales.a

<table>
<thead>
<tr>
<th>Year</th>
<th>Surface flow</th>
<th>% change from inflow to outflowb</th>
<th>Result of t-testc</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>parameters</td>
<td>Inflow</td>
<td>outflow</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1995 – 1998 (four growing seasons)</td>
<td></td>
</tr>
<tr>
<td>Temperature, °C</td>
<td>24.6 ± 0.1 (350)</td>
<td>26.0 ± 0.2 (365)</td>
<td>+5.7</td>
</tr>
<tr>
<td>Turbidity, NTU</td>
<td>24 ± 2 (372)</td>
<td>24 ± 0.8 (391)</td>
<td>-42</td>
</tr>
<tr>
<td>DO, mg L⁻¹</td>
<td>7.4 ± 0.2 (346)</td>
<td>8.8 ± 0.3 (306)</td>
<td>+19</td>
</tr>
<tr>
<td>pH</td>
<td>8.2 ± 0.03 (348)</td>
<td>8.7 ± 0.1 (360)</td>
<td>+6.1</td>
</tr>
<tr>
<td>Conductivity, mS cm⁻¹</td>
<td>540 ± 7 (346)</td>
<td>430 ± 5 (352)</td>
<td>-20</td>
</tr>
<tr>
<td>Redox, mV</td>
<td>360 ± 5 (333)</td>
<td>340 ± 5 (347)</td>
<td>-6</td>
</tr>
<tr>
<td>SRP, mg L⁻¹</td>
<td>85 ± 15 (38)</td>
<td>12 ± 2 (38)</td>
<td>-86</td>
</tr>
<tr>
<td>Total P, mg L⁻¹</td>
<td>182 ± 17 (38)</td>
<td>88 ± 18 (38)</td>
<td>-52</td>
</tr>
<tr>
<td>NO₃ + NO₂, mg L⁻¹</td>
<td>2.6 ± 0.4 (33)</td>
<td>1.2 ± 0.3 (34)</td>
<td>-54</td>
</tr>
<tr>
<td></td>
<td>Mesocosm wetland (1m²)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>1997 – 1998 (two growing seasons)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature, °C</td>
<td>24.4 ± 0.5 (19)</td>
<td>23.1 ± 0.2 (106)</td>
<td>-5.3</td>
</tr>
<tr>
<td>Turbidity, NTU</td>
<td>20 ± 4 (18)</td>
<td>7 ± 1 (102)</td>
<td>-65</td>
</tr>
<tr>
<td>DO, mg L⁻¹</td>
<td>5.6 ± 0.4 (19)</td>
<td>4.8 ± 0.3 (106)</td>
<td>-14.3</td>
</tr>
<tr>
<td>pH</td>
<td>8.1 ± 0.2 (19)</td>
<td>8.5 ± 0.1 (106)</td>
<td>+5</td>
</tr>
<tr>
<td>Conductivity, mS cm⁻¹</td>
<td>508 ± 17 (19)</td>
<td>538 ± 7 (106)</td>
<td>+6</td>
</tr>
<tr>
<td>Redox, mV</td>
<td>400 ± 16 (19)</td>
<td>324 ± 11 (106)</td>
<td>-19</td>
</tr>
<tr>
<td>SRP, mg L⁻¹</td>
<td>60 ± 4 (19)</td>
<td>10 ± 1 (104)</td>
<td>-83</td>
</tr>
<tr>
<td>Total P, mg L⁻¹</td>
<td>133 ± 6 (19)</td>
<td>100 ± 9 (105)</td>
<td>-24</td>
</tr>
<tr>
<td>NO₃ + NO₂, mg L⁻¹</td>
<td>1.7 ± 0.2 (19)</td>
<td>0.6 ± 0.1 (105)</td>
<td>-65</td>
</tr>
</tbody>
</table>

aGrowing season indicates two months (July and August) for full-scale wetland and one month (July or August) for mesocosms.
bIncrease is indicated by plus symbol, decrease by minus symbol.
cNTU, Nephelometric Turbidity Units.
dInflow versus outflow, NS: no significant difference; *: significant difference at a = 0.05

Water due to basin morphology and topography. Moreover, the full-scale wetland can channelize over time especially due to the dominant pumped inflow; thus the water could stay in the wetland basin for a shorter time than the nominal hydraulic retention time calculated here. Retention time is a critical factor for nutrient retention in wetlands (Kadlec and Knight, 1996). The longer retention time of the full-scale wetland in 1996 probably caused the higher amount of nutrients retained in the full-scale wetland relative to other years (Tables 1 and 3).

Flow patterns and mixing

Physical configurations may also be important to be considered in the evaluation of wetland functions compared at two different scales. Internal island or topographic features and preferential flow channels can induce hydraulic inefficiencies on water quality amelioration (Kadlec and Knight, 1996). Large-scale eddies or wind-induced mixing actions, probably unlikely in mesocosms, occur and change the hydraulic conditions in the full-scale wetland. Mesocosms may have more ideal flow pattern (plug flow or well-mixed) due to their small scale by which complete mixing of the water seems possible, whereas the full-scale wetland may have non-ideal flow patterns allowing only intermediate degree of mixing due to channelized flow over a long distance.

Sanford (1997) argued that hydraulic properties of systems such as turbulent mixing might vary through downscaling of mesocosms, thus causing chemical and biological processes to change in the systems. Vertical mixing may be different depending on the depth, water velocity and substrate characteristics. Given relatively low water depth (10 – 30 cm) in both types of wetlands, there does not seem to be much difference of the degree of mixing and its effects on water quality improvement, specifically nutrient retention, of two different wetland systems investigated. Quantitative tests such as tracer analyses would be useful to characterize the hydraulic conditions or hydrodynamics of wetlands to investigate their effects on intrinsic chemical or biochemical processes in further studies.
Table 3. Percent change and statistical comparison of water quality parameters in full-scale wetland and mesocosms over four and two growing seasons, respectively.a

<table>
<thead>
<tr>
<th>Scale (1m²)</th>
<th>% Change from inflow to surface outflowb</th>
<th>Mesocosm wetlands</th>
</tr>
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<tbody>
<tr>
<td>Year</td>
<td>Full-scale wetlands (10,000 m²)</td>
<td></td>
</tr>
<tr>
<td>Temperature, °C</td>
<td>+9.8</td>
<td>+3.9</td>
</tr>
<tr>
<td>Turbidity, NTU²</td>
<td>-55</td>
<td>-70</td>
</tr>
<tr>
<td>DO, mg L⁻¹</td>
<td>+3.2</td>
<td>-5.8</td>
</tr>
<tr>
<td>pH</td>
<td>+10.7</td>
<td>+1.5</td>
</tr>
<tr>
<td>Conductivity, mS cm⁻¹</td>
<td>-23</td>
<td>-16</td>
</tr>
<tr>
<td>Redox, mV</td>
<td>-10</td>
<td>-0.4</td>
</tr>
<tr>
<td>SRP, mg L⁻¹</td>
<td>-60</td>
<td>-93</td>
</tr>
<tr>
<td>Total P, mg L⁻¹</td>
<td>-70</td>
<td>-70</td>
</tr>
<tr>
<td>NO₃ + NO₂, mg L⁻¹</td>
<td>-62</td>
<td>-38</td>
</tr>
</tbody>
</table>

|                   | Full-scale wetlands (10,000 m²)         | Mesocosm wetlands |
|                   | NS  | NS  | NS  | NS  | NS  | NS  | NS  |

aGrowing season indicates two months (July and August) for full-scale wetland and one month (July or August) for mesocosms.
bIncrease is indicated by plus symbol, decrease by minus symbol.
cNTU, Nephelometric Turbidity Units.
dInflow versus outflow; NS: no significant difference; *: significant difference at α = 0.05

### Plant productivity

Mesocosms can distort important variables such as macrophyte productivity that may control the dynamics of full-scale constructed wetlands (Busnardo et al., 1992; Boynton et al., 1997). The same artifact of mesocosms was observed in this study. Plant stems leaned over the walls of mesocosms receiving sunlight from an area larger than that of the mesocosm resulted in higher biomass production because of a higher edge/area ratio than in the full-scale wetland. That is to say, the mesocosms were “effectively” larger than 1 m². Aquatic macrophytes have important roles in nutrient retention in wetland systems (Breen, 1990; Rogers et al., 1990; Kadlec and Knight, 1996), but “pot-bound” plants in our small-scale wetlands did not allow any space in surface water after one year of operation and eventually led to potentially more reduced conditions in mesocosm sediments.

Chen et al. (1997) pointed out periphyton growth on container walls in mesocosms is an intrinsic artifact that must be considered when interpreting results from mesocosms since periphyton grown on the walls of mesocosms could account for over 50% of total ecosystem gross primary productivity (GPP) and biomass. Periphyton growth on the walls of our mesocosm wetlands, however, was negligible through this study. Light attenuation caused by macrophytes in the mesocosms limited algal growth in the containers (e.g. Berg et al., 1999), resulting in relatively low water column productivity as reflected in no change of the dissolved oxygen concentration through the mesocosm wetlands over two years (Table 2).

![Figure 3. Phosphorus concentration of inflow and outflow of the full-scale wetland over a 4-year period and mesocosm experimental wetlands over a 2-year period (mean ± S.E.). The same letters among the treatments indicates no statistical difference.](image-url)
Table 4. Peak biomass of *S. tabernaemontani* (mean ± S.E.) in full-scale wetland over a 4-year period and mesocosms over a 2-year period.

<table>
<thead>
<tr>
<th>Scale</th>
<th>Full-scale wetland (10,000 m²)</th>
<th>Mesocosm wetlands (1 m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aboveground biomass, g m⁻²</td>
<td>na a na 359± 28 401± 30</td>
<td>121 ± 11 b 425 ± 33</td>
</tr>
<tr>
<td>Belowground biomass, g m⁻²</td>
<td>na</td>
<td>na 359 b 401 b</td>
</tr>
<tr>
<td>Plant cover, % c</td>
<td>13 39 54 55</td>
<td>- essentially 100 -</td>
</tr>
<tr>
<td>Total biomass, g m⁻²</td>
<td>114 b 436 b 718 802</td>
<td>549 ± 24 1,229 ± 78</td>
</tr>
<tr>
<td>% cover of <em>S. tabernaemontani</em></td>
<td>13 35 44 37</td>
<td>100 100</td>
</tr>
</tbody>
</table>

a Data not available.
b Estimated; total biomass (for full-scale in 1995 and 1996) = 220.57 X10^0.0030657 * maximum stem length, cm), n = 5, R² = 0.98 (Weihe and Mitsch, 1996).
c Estimated by analysis of aerial photography for the whole plant communities of the full-scale wetland.

**Physicochemistry and nutrient retention**

The greater macrophyte biomass in the mesocosm wetlands after the first year led to decreased water temperature by blocking sunlight, less surface turbulence through wind action, and therefore less oxygen diffusion into water, and less water column productivity. These conditions may have affected sediment oxygenation and stimulated more reduced conditions in the mesocosm sediments, which subsequently influence nutrient transformations and regeneration in the sediments (Addiscott and Devel, 1992). A negative relationship between dissolved oxygen and total phosphorus in surface outflow of the mesocosm wetlands was detected (r = -0.36, p = 0.05).

Wetland sediments become anaerobic after they are flooded with water, so reduced conditions are the typical feature of wetlands (Mitsch and Gosselink, 2000). This reduced condition influences phosphorus dynamics in anaerobic sediments because the inorganic phosphorus adsorbed with iron and aluminum oxyhydroxides can be released back to the water (Patrick et al., 1973; Bostrom et al., 1982). This may be part of explanation for the significant export of phosphorus in the second year. Physical proximity of the sediment layer to the water column in the mesocosms relative to the full-scale wetland is more likely to cause physically- or biologically-mediated processes such as resuspension of sediments, even though wind-induced turbulence is less in the mesocosms.

Relatively high nitrogen removal in both scales of wetlands was probably due to denitrification as anaerobic sediments in wetlands are the perfect habitats for various denitrifying bacteria to reduce nitrates and transform them into nitrogen gas (N₂), which is lost into the atmosphere. Higher surface water temperature in the full-scale wetland would lead to potentially higher rates of denitrification. On the other hand, denitrification is enhanced with low DO and more organic C produced after the first growing season in the mesocosms.

**Ecosystem complexity**

Scale is defined broadly to include complexity of the system as well as space and time (Petersen et al., 1999). Figure 5 shows conceptually the components and forcing functions of the two different wetland systems compared in our study. Mesocosms are models of small patches of the full-scale counterpart, and can only support a relatively small number of components depending on their size, thus reducing their ecological complexity relative to a full-scale wetland. The mesocosms we used do not contain fish, waterfowl, muskrats and other mobile species as active components in the system. This altered complexity of system being studied affects biogeochemical functions of the system, especially pathways of nutrient cycling as shown in Figure 5. However, it may not necessary to have all of the components in Figure 5a to simulate a full-scale system with mesocosms. Moreover, achieving the proper density of large animals in small mesocosms is essentially impossible.

**Figure 4.** Total phosphorus removal versus hydraulic loading rate from the full-scale and mesocosm wetlands during growing seasons. Data between June through October were used for each year depending on the availability of the data.

As to the predictability of how system works at different levels of scale (spatial and temporal), the question goes to the uncertainty attached to our knowledge of the dominant forces and the initial state of the system being changed at different scales (Addiscott, 1998). The wetlands studied at two different scales contain the same relative forcing.
functions of sunlight and water and nutrient inflow and main components such as plants, sediments and water that allow self-organization of the system to manifest itself. But the small mesocosms are not open to biological transport of propagules by ducks, geese, muskrats, and other large animals and aerial and water inflow of propagules might be somewhat less likely with the plumbing and location of the mesocosms. Adey et al. (1996) argued that functions of the system should not be judged on presence of particular components but rather on presence of major structural components allowing self-design and self-organization of the system. But the presence of biological components such as large animals sometimes suggest new avenues of propagule introduction.

**Scale considerations of mesocosms**

Many experiments previously conducted by mesocosms have failed to report exact spatio-temporal scale used (Petersen et al., 1999). Lack of care on the scale at which the experiments are conducted may largely be responsible for the ambiguities surrounding mesocosm results. Underwood (1986) reported that some organisms might display different behavior when exposed to alternative experimental conditions and especially to confinement. Stephenson et al. (1984), Solomon et al. (1989), and Flemer et al. (1995) showed that mesocosm size could affect results. Schindler (1998) mentioned that a full-scale ecosystem loses its complexity when scaled down to a container, so that such features as air-water and sediment-water exchanges and the activities of wide-ranging organisms may not be included. Earlier, Lund (1972) showed that phytoplanktonic populations in undisturbed enclosures were significantly different from their developments in a lake. A possible explanation for this difference was the elimination of horizontal advection by mechanical barriers, causing difference in turbulence, light, nutrient concentrations, primary production, and both plankton biomass and species composition (Bloesch et al., 1988). Hence, there is a danger that work conducted in mesocosm environments produces replicated, well-controlled results of artifacts—processes that may not actually occur in the field (Lawton, 1999).

Based on our study, we noticed such anomalies of mesocosms that may affect further interpretation of mesocosm results as different physicochemical trends, rapidly decreasing phosphorus retention, and higher biomass production. We believe that it is not readily possible to simulate all realistic, physical and biological conditions and the interactions of both in mesocosms (i.e. realistic water mixing, turbulence at the sediment-water interface of the full-scale wetland) due to their small sizes and boundary conditions (wall effects).

Comparison of the two wetland systems in our study was not natural system versus artificial system. Both systems were supported by artificially maintained hydrology (pumped inflow) yet both developed naturally with no other human intervention. In terms of system performance for particular functions, the mesocosms provided replicated measurements on basic ecosystem processes that can be studied over a reasonable short time period, regardless of their artifacts and less realistic physical conditions. It is nevertheless critical to note the artifacts of mesocosms found in our study. Adey and Loveland (1991) also suggested scaling considerations as important for successful mesocosm design. We agree and recommend that study of scaling effects of mesocosms continue through multi-scale experimental design or scale comparisons. Otherwise we are running statistically rigorous studies that may have strong statistics but little reality.

**Temporal scale**

It seems reasonable to use this kind of mesocosm approach to study specific biogeochemical processes of wetland ecosystem for no more than two years. Giddings and Eddlemon (1979) reported some ecological and experimental properties of complex aquatic microcosms and suggested a termination of microcosm after a certain amount of time (about 30 days for the food chain microcosm they used). Temporal scales may be limited due to the rapid change of the initial conditions of the system over time in mesocosm scale. Mesocosms used in this study became rapidly pot-bound with plants in two growing seasons, potentially distorting the processes being investigated. We need to consider the duration of mesocosm experiment based on the size of system being used for the study. We may have to shorten the time span during which the mesocosm experiment is being conducted. Efforts to find quantitative scaling relationships between size and time period are needed.

**Conclusions**

Mesocosms are often used to study ecological development, biogeochemical processes or nutrient dynamics in wetland systems. Mesocosms allow replicability and repeatability of experiments at a much lower cost than do full-scale ecosystems. Practical constraints such as cost, availability of equipment, and land availability are likely more important determinants of system size and experimental duration in many cases of ecological research. The pair of full-scale wetlands of our study cost $ 310,000 for construction and about $10,000 per year for operation and maintenance. In contrast, mesocosms cost $70 each ($700 for a set of 10) and about $500 annually for operation of a set. And mesocosms give more flexibility in our experimental designs.

The outcomes of our study, however, suggest that we consider ‘scale’ before results from mesocosm studies are generalized to full-scale wetlands. Studies on the scaling effects of wetland mesocosms should be continually conducted to provide useful information on system size and experimental duration of mesocosms being used. Investigating and reporting the artifacts of mesocosms and any difference between the studies conducted at different scales will be valuable to better design and interpret mesocosm experiments in future ecological research on
wetland functions. More critically, quantitative efforts are needed to understand ecological consequences of the differences found in scale comparisons so that we can reasonably extrapolate results from experimental mesocosms to full-scale ecosystems. Scaling theory can be integrated with the empirical approach we took in this study to assist in this extrapolation.

Acknowledgments

We appreciate the assistance of dozens of students and staff of the Olentangy River Wetland Research Park for water, vegetation, and hydrology sampling and measurements of the full-scale wetland through the years.

Figure 5. Conceptual diagram of two experimental wetlands at different spatial scales. Simulation illustrated processes involved in phosphorus retention by these wetlands.
Table 5. Summary of characteristics of two wetland scales compared in the study for growing season.

<table>
<thead>
<tr>
<th></th>
<th>Full-scale</th>
<th>Mesocosm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spatial scale</td>
<td>10, 000 (m(^2))</td>
<td>1 (m(^2))</td>
</tr>
<tr>
<td>Source soil</td>
<td>identical</td>
<td></td>
</tr>
<tr>
<td>Source water</td>
<td>identical</td>
<td></td>
</tr>
<tr>
<td>Hydrology / Hydraulics</td>
<td></td>
<td></td>
</tr>
<tr>
<td>HLR &amp; HRT</td>
<td></td>
<td>similar</td>
</tr>
<tr>
<td>Turbulence</td>
<td>moderate to high</td>
<td>low</td>
</tr>
<tr>
<td>Mixing</td>
<td>moderate</td>
<td>moderate to high</td>
</tr>
<tr>
<td>Plants</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Macrophytic biomass</td>
<td>800 g m(^{-2})</td>
<td>1200 g m(^{-2})</td>
</tr>
<tr>
<td>Percent cover</td>
<td>~ 60 %</td>
<td>~ 100 %</td>
</tr>
<tr>
<td>Species richness</td>
<td>moderate</td>
<td>low</td>
</tr>
<tr>
<td>Algal mat</td>
<td>moderate</td>
<td>low</td>
</tr>
<tr>
<td>Water quality change</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>increase</td>
<td>decrease</td>
</tr>
<tr>
<td>Turbidity</td>
<td>decrease</td>
<td>decrease</td>
</tr>
<tr>
<td>Dissolved oxygen</td>
<td>increase</td>
<td>no change or decrease</td>
</tr>
<tr>
<td>pH</td>
<td>increase</td>
<td>increase</td>
</tr>
<tr>
<td>Conductivity</td>
<td>decrease</td>
<td>increase or no change</td>
</tr>
<tr>
<td>Nutrient retention capacity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total phosphorus</td>
<td>moderate (fluctuating)</td>
<td>low (decreasing)</td>
</tr>
<tr>
<td>Soluble reactive phosphorus</td>
<td>similar (very high)</td>
<td></td>
</tr>
<tr>
<td>Nitrate plus nitrite</td>
<td>similar (moderate to high)</td>
<td></td>
</tr>
<tr>
<td>Effective temporal scale</td>
<td>long (years)</td>
<td>short (weeks to months)</td>
</tr>
<tr>
<td>Ecosystem complexity</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spatial heterogeneity</td>
<td>moderate</td>
<td>low to none</td>
</tr>
<tr>
<td>Ecological complexity</td>
<td>moderate to high (developing)</td>
<td>low</td>
</tr>
</tbody>
</table>

References


