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Scaling considerations of mesocosm wetlands in simulating large created freshwater marshes

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Abstract

To explore the effects of experimental scale on ecological functions in wetlands, flow-through mesocosm wetlands (1 m^2) were compared over the first two growing seasons to a large, created, flow-through wetland (10 000 m^2) over four growing seasons. Hydrology was generally similar with mean hydraulic loading rates of 7.8 cm day^{-1} for the large wetland (excluding an extensive flooding year of 1995) and 6.3 cm day^{-1} for mesocosms. Mean hydraulic retention time was 2.1 days for the large wetland and 1.7 days for mesocosms. Temperature of surface water decreased slightly from inflow to outflow in mesocosms, while it increased in the large wetland. Conductivity of water in mesocosms showed no significant changes from inflow to outflow, while it decreased significantly in the large wetland. Phosphorus was retained effectively in the large wetland for 3 of 4 years and was retained in the mesocosms during the first of 2 years. Phosphorus was exported in the second year in the mesocosms, when dissolved oxygen (DO) and redox potential dropped significantly. Net aboveground primary productivity was similar between mesocosm wetlands ($\sim$ 353 g m^{-2} $year^{-1}$) and the large wetland ($\sim$ 380 g m^{-2} $year^{-1}$). Extensive shading with no open space may have led to cooler water temperatures and lower water column productivity in the densely vegetated mesocosms than in the large wetland in the second year. Less surface turbulence in the mesocosms due to less fetch affected DO too. These conditions may have stimulated development of reduced conditions in mesocosm soils more rapidly than in the large wetland, thereby causing the release of phosphorus. Scale of experiments and mesocosm artifacts must be considered before the results from mesocosm studies are generalized to large field-scale wetlands.

Keywords: Scaling; Scale; Mesocosm; Constructed wetlands; Phosphorus retention; Net aboveground primary productivity; Ecosystem complexity; Olentangy River Wetland Research Park

1. 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,

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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., 2001; Svengsouk and Mitsch, 2001). Mesocosms provide a means of conducting ecosystem-level experiments under replicated, controlled, and repeatable conditions at a 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- and mesocosm approaches in ecological studies because they contain intrinsic artifacts (e.g., wall effects) 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-scale studies are conducted (Schindler, 1998) and the limitations of mesocosm studies understood.

Criticism of mesocosm-scale studies has stimulated the use of 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-scale experiments 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, large-scale ecosystem experiments are difficult to replicate 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 (Odum, 1984; Bloesch et al., 1988; Carpenter, 1988; Levin, 1992; Schneider, 1994; Carpenter et al., 1995; Carpenter, 1996; Petersen et al., 1997; Fairweather and Quinn, 1998; Peterson and Parker, 1998; Petersen et al., 1999; Whittaker, 1999; Gardner et al., 2001). 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 large ecosystem-scale research and on the research questions being investigated. Scale can change nutrient cycling, the number of trophic levels, the number of species within trophic levels, habitat types, and connectivity between habitats (Beyers and Odum, 1993). Yet the advantages of meso-scale experiments, namely low cost and replication possibilities, lead to the frequent use of these ecosystem 'models.'

No studies to our knowledge 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 mesocosm wetlands (1 m^2) with a large experimental marsh (10 000 m^2) under similar environmental conditions (hydrology and water chemistry of inflow) to elucidate positive and negative aspects of using mesocosms in wetland science. Mesocosm wetlands were compared for hydrology and water quality changes over the first two growing seasons with a large, created experimental wetland over its first four growing seasons. Macrophyte productivity was also compared between the two types of wetlands over two growing seasons.

2. Materials and methods

2.1. A large wetland (10 000 m^2)

A whole-ecosystem, long-term wetland experiment was started in 1994 with two 10 000 m^2 basins constructed on the floodplain of the Olentangy River in Columbus, Ohio (Fig. 1(a); Mitsch et al., 1998) at the Olentangy River Wetland Research Park (ORWRP). River water is fed to this wetland at rates of 20–40 m $year^{-1}$ (Mitsch et al., 1998). Prior to wetland construction, the soil in the wetland basins was classified as Ross series, loamy mesic Cumulic Hapludoll. Although the large-scale, long-term wetland experiment began in 1994, the year of 1994 can be regarded as an acclimation period, as macrophytes were introduced in May 1994. There was no significant macrophytic vegetation cover in the large wetland until 1995; therefore we chose four early years (1995 through 1998) for the comparison of hydrology and water quality with the experimental mesocosm wetlands. Seasonal effects were excluded from the study by comparing only growing season data (July and August). Mitsch et al. (1998), Mitsch and Bouchard (1998), and Bouchard and Mitsch (1999) describe macrophyte productivity and development in these experimental wetlands during this study. Net aboveground primary productivity (NAPP) was estimated in the 'planted' wetland (Wetland 1; bottom basin in Fig. 1(a)) by harvesting peak biomass at the end of two growing seasons (1997 and 1998) and corrected for the percent of area of macrophyte

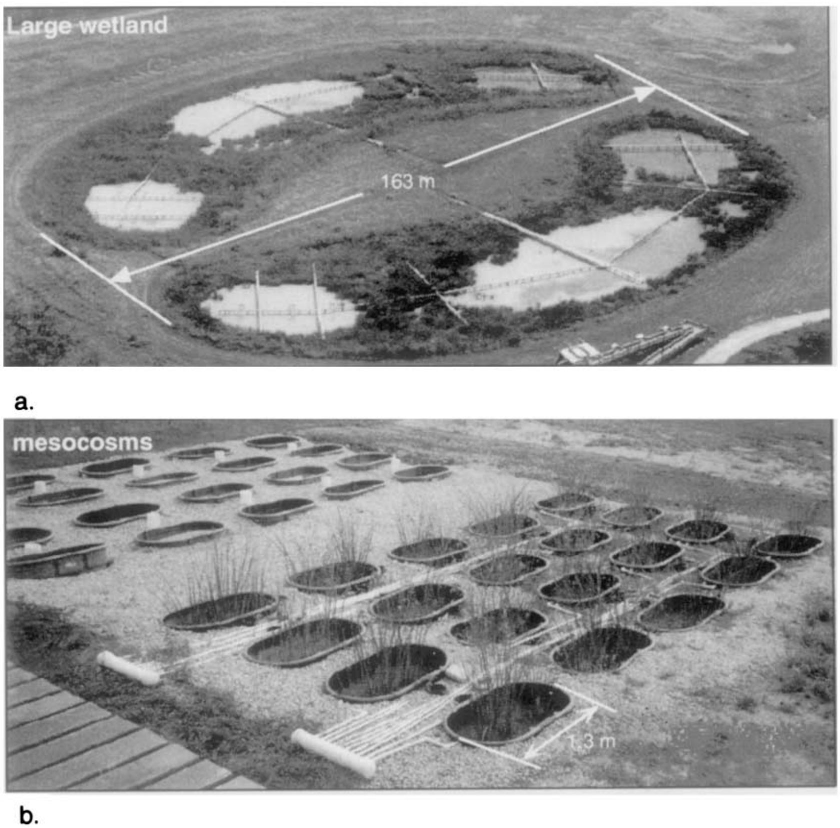

Fig. 1. Study sites at Olentangy River Wetland Research Park at the Ohio State University, Columbus, Ohio illustrating: (a) two large (1-ha) flow-through experimental wetland basins. The bottom basin was used in this study. (b) set of flow-through mesocosms (each 1 m^2) used in this study.

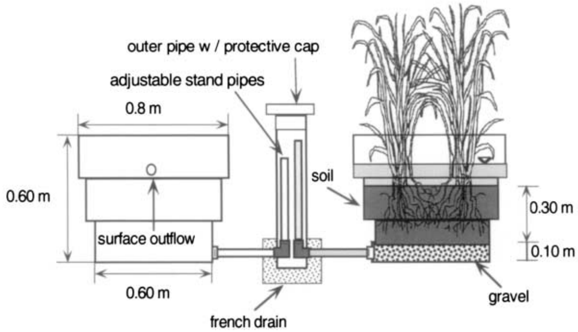

Fig. 2. Schematic diagram of a pair of mesocosms used in the study (from Ahn et al., 2001).

cover for the comparison of macrophyte productivity with mesocosms. For the comparison, all data representing the large wetland were obtained from Wetland 1.

The experimental design, site description, and hypothesis of the large wetland 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 changes through the large wetlands have been documented (cf. Mitsch et al., 1998; Nairn and Mitsch, 2000; Spieles and Mitsch, 2000). Algal mat development in the early years is described in Wu and Mitsch (1998).

2.2. Mesocosm wetlands (1 m^2)

Experimental mesocosms ($= 0.8 \times 1.3 \times 0.6$ m^3 polyethylene tubs) were installed at the ORWRP starting in the spring of 1995 to allow more controlled and replicated experiments with wetlands (Fig. 1(b)). A set of ten flow-through mesocosms (Fig. 1(b); Fig. 2) was used in this study for two growing seasons (1997 and 1998) under hydrologic conditions similar to the large wetland while serving as controls for another experiment (Ahn et al., 2001). 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 site soil as in the large wetland. Soil was not compacted so some initial settling occurred. Three *Schoenoplectus tabernaemontani* (soft-stem bulrush) rhizomes, a common wetland plant in the large wetland ($>80\%$ of total plant cover and $>90\%$ of total NAPP in 1997; Mitsch and Bouchard, 1998), were planted into each mesocosm. The rhizomes were equally spaced lengthwise in the mesocosm, pressed just below the surface of moist soil, and buried to 3 cm depth. The vegetation species in both scales were from the same source of plant material (Wildlife Nurseries, Wisconsin), so it is unlikely that there is any difference in ecotype or genotype of the plants between the two scales. A water delivery system to the mesocosms was constructed through a series of manifolds and valves which distributed similar volumes of water pumped from the Olentangy River to each of the ten mesocosms (Fig. 1(b)). 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. That rate was the same as the flow rate going into the large wetland and the river water feeding the mesocosm came from the same source of water feeding the large wetland. Because steady flow rates at this scale were difficult to maintain, a pulse system was used in the second year to deliver a similar, per-day volume, 1 h day^{-1}. 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. Water levels and flow rates varied within only 15% among each of the ten mesocosms. Standing water levels of about 10 cm were maintained during this comparison.

2.3. Sampling and analysis of water quality

Water sampling for nutrient analyses is conducted in the large wetland every week, whereas all other water quality parameters (temperature, dissolved oxygen (DO), pH, conductivity, and redox potential) are measured through twice-per-day manual samplings. The sampling scheme and methodology used for water quality analysis in the large wetland are summarized in Nairn and Mitsch (2000) and Spieles and Mitsch (2000). We used 2 months (July and August) of nutrient and water quality data each year over a 4-year period (1995 through 1998) from the large wetland. Water samples from the large wetland were analyzed in the same way through the years as with mesocosm samples (see the next paragraph) with two exceptions: nutrients in water samples collected from the large wetland 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 large wetland in 1996 was measured with a Solomat 520C monitor and an Orion ion selective electrode (Spieles and Mitsch, 2000).

Mesocosm water was sampled three times per week for 1 month over two growing seasons. A Hydrolab H20G Multiparameter Water Quality Data Probe was used to measure temperature, DO, pH, conductivity, and redox potential through the period of experiments. The H20G probe was calibrated weekly during the experiments. Surface outflow samples were collected directly from the outlets of each mesocosm (Fig. 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 μm filter and placed in a freezer for later soluble reactive phosphorus (SRP) analysis. Filters were soaked for ≈ 24 h in distilled water to remove contamination. Unfiltered subsamples were preserved by acidification with 2 ml 36 N H_2SO_4 per l of sample (to $pH < 2$) immediately upon return to the lab. 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 performed on the LACHAT QuickChem IV Flow Injection Analysis 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.

2.4. Net aboveground primary productivity of macrophytes

Large wetland—NAPP of macrophytes in the large wetland was estimated by harvesting peak biomass at the end of two growing seasons in 1997 and 1998 by Mitsch and Bouchard (1998) and Bouchard and Mitsch (1999). Plant cover (%) estimated by August aerial photography for the large wetland was multiplied by the NAPP for the same year to estimate effective NAPP for the large wetland.

Mesocosms—total number of stems and stem lengths were measured weekly in each mesocosm over two growing seasons in 1997 and 1998. For average stem length, 20 randomly chosen stems were measured for each mesocosm. Cumulative stem length (CSL) was calculated as the average stem length × number of stems. A regression equation was developed between NAPP and CSL from second-year harvested mesocosms (see below) to estimate the NAPP of the first year.

$$\mathrm{NAPP} = (0.01655 \times \mathrm{CSL}) - 134.87 \quad (n = 10,\ r^2 = 0.91), \tag{1}$$

where NAPP, net aboveground primary productivity (g-dry wt m^{-2} $year^{-1}$); CSL, cumulative stem length (cm in 1 m^2).

At the end of the second growing season (1998), plants in the mesocosms were cut at ground level, placed in plastic bags and weighed in the field with a hanging balance (accuracy ± 40 g). Subsamples were taken to a laboratory where both wet and dry weights were determined. Dry/wet ratios were multiplied by total wet weight of the biomass harvested to estimate each dry weight production afterward.

Macrophytes densely colonized the mesocosm tubs in the second year with leaves overhanging well over the sides of the tubs (Fig. 3). This effect has been noted in previous mesocosm studies (Busnardo et al., 1992) and leads to an error in attributing all the plant biomass to the area of the mesocosm. The effect is due to a large edge to area ratio for the small mesocosms. To compare NAPP between the large wetland and the mesocosms, peak biomass from mesocosm wetlands in the second year was corrected for this overhang. A correction factor (c) for the macrophyte overhang was calculated on the assumption that the volume occupied by aboveground macrophytes in mesocosms is a rectangular 'container.' The extra volume created by the overhang in addition to the rectangular container was calculated as a triangular volume (Fig. 3). The length (s) of macrophyte overhang that deviated from the main rectangular dimension was 0.1 m based on field observations and that figure was used in the calculation of the triangular volumes.

$$c = \frac{V_r}{V_r + V_e}, \tag{2}$$

where c, correction factor (unitless); V_r, rectangular volume occupied by the aboveground biomass of macrophyte and attributed only to the area of the mesocosm $= w \times l \times h$ (m^3) (Fig. 3); V_e, additional triangular volume due to macrophyte overhang $= s \times h \times (l + w)$ (m^3) (Fig. 3); w, width of mesocosm (m); l, length of mesocosm (m); h, plant height (m); s, extra length of plant overhang (m).

The correction factor was multiplied by harvested biomass to estimate corrected NAPP for the mesocosm in the second year. The correction factor for the large wetland and the first-year mesocosms was assumed 1.0 since their relative overhang areas were extremely small.

2.5. Statistical analysis

For surface water quality data, averages of all the parameters measured were calculated and then used for statistical analysis. Repeated measures

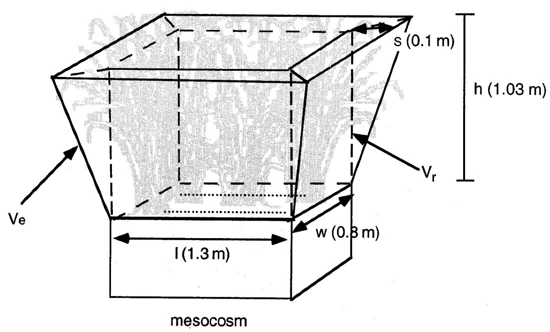

Fig. 3. A mesocosm wetland and its macrophyte overhang observed in this study. w, width of mesocosm; l, length of mesocosm; h, plant height; s, extra length due to plant overhang.

from the large wetland were used as replicates since only one large wetland was compared with ten mesocosms. Percent change of water quality parameters from inflow to outflow was calculated and the significance of the changes was tested via two-sample unpaired t-tests assuming unequal variance at $P < 0.05$. The hydrologic condition in 1995 in the large wetland was quite different from the other years due to extensive flooding events during the growing season. Since hydrologic conditions are closely related to water quality functions of wetlands, we calculated the water quality change over the large wetland for each growing season as well as over a 4-year period as a pooled average.

The coefficient of variation (CV = standard deviation/mean × 100%; Steel et al., 1997) of each parameter of inflow and outflow waters from the large wetland and mesocosms was calculated to compare variability between the two different scales. If the large wetland has a much higher CV than that of the mesocosms for a specific parameter, comparing the averages of that parameter between the two scales should not be used to attribute any differences found to 'scale' since other potential factors than size may obscure our interpretation. The variability of mesocosm and large wetland data helped us decide how convincingly the differences found can be attributed to scale versus other factors including sampling error.

A two-way ANOVA by the General Linear Model procedure in SAS (SAS Institute, 1988) was used to compare the large wetland and mesocosms for their effective NAPP over two growing seasons (1997 and 1998). Tukey's multiple tests were chosen to test all pairwise contrasts of means for significance at $P < 0.05$ (Steel et al., 1997).

3. Results

3.1. Hydrology and nutrient loading

The hydraulic loading rates (HLR) for the large wetland (excluding the flooding year of 1995) and the mesocosms were similar (6–8 cm day^{-1}, respectively; Table 1). Two natural flooding events

Table 1
Hydraulic and nutrient loading rates, water depth, and retention time of the large wetland and mesocosms over four and two growing seasons, respectively

	Large wetland (10 000 m^2)				Mesocosm wetlands (1 m^2)	
	1995[a]	1996	1997	1998	1997	1998
Hydraulic loading rate (cm day^{-1})	23.8	8.2	6.2	9.1	7.3	5.3
Mean water depth (cm)	44.4	27.9	10	14	10.8	10.2
Water volume (average, m^3)	4440	2790	1000	1400	0.11	0.10
Hydraulic retention time (days)	1.9	3.4	1.6	1.6	1.5	1.9
Phosphorus loading rate (mg-P m^{-2} day^{-1})	56.7	16.2	9.9	14.0	10.2	6.7
Nitrate loading rate (mg-N m^{-2} day^{-1})[b]	390	400	90	210	100	100

[a] Higher hydraulic loading due to flooding event (June 27th and August 8th, 1995).
[b] Nitrogen as NO_3+NO_2.
Growing season indicates 2 months (July and August) for the large wetland and 1 month (July or August) for mesocosms.

(overflow from the river) occurred on June 27th and on August 8th of 1995 in the large wetland, increasing the HLR during the 1995 growing season to 23.8 cm day^{-1}. Retention time of water ranged from 1.5 to 2 days for both scales for every year except when the large wetland had a retention time of more than 3 days in 1996.

Flooding in 1995 in the large wetland increased phosphorus loading rates in the growing season to 57 mg-P m^{-2} day^{-1}; otherwise the average value for the other years was 13 mg-P m^{-2} day^{-1} (Table 1). Phosphorus loading rates for the mesocosms ranged from 7 to 10 mg-P m^{-2} day^{-1}. Nitrate-nitrogen loading ranged from 90 to 400 mg-N m^{-2} day^{-1} for the large wetland and averaged 100 mg-P m^{-2} day^{-1} in both years for the mesocosms.

It is difficult to calculate the exact water velocity of the two wetlands due to many boundary and changing conditions. Water velocity was roughly estimated for both types of wetlands by dividing the volumetric surface water flow (m^3 day^{-1}) at the mid point of the wetland or mesocosm by the cross sectional area (water depth $\times$ width, m^2) of the wetlands. With this assumption, mean water velocity was 0.54 m day^{-1} for the large wetland and 0.49 m day^{-1} for the mesocosms. The large wetland showed relatively slower movement of flow in 1996 (0.23 m day^{-1}) when the retention time of water was longer (3 days vs. 1.5–2 days in other years).

3.2. Physicochemistry

The large wetland and mesocosms showed opposite water temperature trends. The large wetland showed a significant and consistent increase of temperature of the water from inflow to outflow over the 4-year period (6% increase on average) while mesocosms showed a significant decrease over a 2-year period (5% decrease on average) (Tables 2 and 3). DO increased significantly through the large wetland in 2 of the 4 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). pH increased significantly in both the large and mesocosm wetlands, probably due to photosynthetic activity in their water column (Table 2). Conductivity in the mesocosm wetlands showed no significant change overall (Table 2), but did increase in the first year and decrease in the second year (Table 3). The large wetland showed a significant and consistent decrease of conductivity, which averaged 20% through the years (Table 2). This decrease is partially related to extensive calcite precipitation verified in this experimental wetland (Liptak, 2000). Redox potential of water flowing through both the large and mesocosm wetlands decreased each year, thus reflecting an anaerobic condition of wetland sediments. The decrease was generally 7–12%. But redox potential decreased dramatically by more than 40% in the mesocosm wetlands in year 2

(Tables 2 and 3). This second year effect in the mesocosm turned out to be significant for nutrient retention described below.

3.3. Nutrient retention

Both types of wetlands retained nutrients in most growing seasons observed (Tables 2 and 3). SRP decreased by 80% on average in both mesocosms and the large wetland (Tables 2 and 3). Retention of TP averaged 52% over 4 years for the large wetland and 24% over 2 years for the mesocosm wetlands (Table 2). There was no TP retention observed in the 1997 growing season for the large wetland and a significant TP export (25%) in the second year of the mesocosms (Table 3). The export of TP in the second year of the mesocosm corresponds to the dramatic decrease in redox potential noted for the mesocosms in the same year. Nitrate retention was significant through the years in the two different wetlands, averaging 54% for the large wetland and 65% for the mesocosms (Table 2).

Table 2
Water quality (mean ± S.E., (*n*)) of inflows and outflows, and their coefficient of variance (CV) during the growing seasons of both the large and mesocosm wetlands

	Surface outflow				% Change from inflow to outflow[b]	Result of *t*-test[c]
	Inflow	CV (%)[a]	Outflow	CV (%)		
Large wetland (10 000 m²)						
1995–1998 (four growing seasons)						
Temperature (°C)	24.6 ± 0.1 (350)	7	26.0 ± 0.2 (365)	13	+5.7	*
DO (mg l^{-1})	7.4 ± 0.2 (346)	38	8.8 ± 0.3 (306)	63	+19	*
pH	8.2 ± 0.03 (348)	6	8.7 ± 0.1 (360)	12	+6.1	*
Conductivity (μs cm^{-1})	540 ± 7 (346)	22	430 ± 5 (352)	22	−20	*
Redox (mV)	360 ± 5 (333)	25	340 ± 5 (347)	28	−6	*
SRP (μg l^{-1})	85 ± 15 (38)	105	12 ± 2 (38)	99	−86	*
Total P (μg l^{-1})	182 ± 17 (38)	56	88 ± 18 (38)	125	−52	*
NO_3+NO_2 (mg l^{-1})	2.6 ± 0.4 (33)	90	1.2 ± 0.3 (34)	127	−54	*
Mesocosm wetlands (1 m²)						
1997–1998 (two growing seasons)						
Temperature (°C)	24.4 ± 0.5 (19)	8	23.1 ± 0.2 (106)	7	−5.3	*
DO (mg l^{-1})	5.6 ± 0.4 (19)	30	4.8 ± 0.3 (106)	56	−14.3	NS
pH	8.1 ± 0.2 (19)	9	8.5 ± 0.1 (106)	11	+5	*
Conductivity (μs cm^{-1})	508 ± 17 (19)	14	538 ± 7 (106)	13	+6	NS
Redox, (mV)	400 ± 16 (19)	18	324 ± 11 (106)	35	−19	*
SRP (μg l^{-1})	60 ± 4 (19)	26	10 ± 1 (104)	98	−83	*
Total P (μg l^{-1})	133 ± 6 (19)	18	100 ± 9 (105)	93	−24	*
NO_3+NO_2 (mg l^{-1})	1.7 ± 0.2 (19)	49	0.6 ± 0.1 (105)	82	−65	*

[a] CV (coefficient of variation) = (standard deviation/mean) × 100.
[b] Increase is indicated by plus symbol, decrease by minus symbol.
[c] Inflow vs. outflow, NS: no significant difference; *: significant difference at $\alpha = 0.05$.
Growing season indicates 2 months (July and August) for the large wetland and 1 month (July or August) for mesocosms.

Table 3
Percent water chemistry changes from inflow to outflow and their statistical significance in the large wetland and mesocosms over four and two growing seasons[a], respectively

	% Change from inflow to surface outflow[b]					
	Large wetland (10 000 m^2)				Mesocosm wetlands (1 m^2)	
	1995	1996	1997	1998	1997	1998
Temperature (°C)	+9.8	+3.9	+4.0	+3.7	−6.4	−4.7
DO (mg l^{-1})	+3.2	−5.8	+26	+56	+0.2	−56
pH	+10.7	+1.5	+7.1	+4.8	+4.2	+1.6
Conductivity (μs cm^{-1})	−23	−16	−21	−18	+11	−5
Redox (mV)	−10	−0.4	−7.6	−12	−7	−41
SRP (μg l^{-1})	−60	−93	−80	−91	−86	−82
Total P (μg l^{-1})	−70	−70	+35	−62	−53	+25
NO_3+NO_2 (mg l^{-1})	−62	−38	−96	−63	−62	−62
	Rate of t-test[c]					
	Large wetland (10 000 m^2)				Mesocosm wetlands (1 m^2)	
	1995	1996	1997	1998	1997	1998
Temperature (°C)	*	*	*	*	NS	NS
DO (mg l^{-1})	NS	NS	*	*	NS	*
pH	*	NS	*	*	NS	NS
Conductivity (μs cm^{-1})	*	*	*	*	*	*
Redox (mV)	*	NS	*	NS	*	*
SRP (μg l^{-1})	*	*	*	*	*	*
Total P (μg l^{-1})	*	*	NS	*	*	*
NO_3+NO_2 (mg l^{-1})	*	*	*	NS	*	*

[a] Growing season indicates 2 months (July and August) for the large wetland and 1 month (July or August) for mesocosms.
[b] Increase is indicated by plus symbol, decrease by minus symbol.
[c] Inflow versus outflow; NS: no significant difference; *: significant difference at $\alpha = 0.05$

3.4. Macrophyte productivity

NAPP of macrophytes in the mesocosms estimated in the second year after overhang correction was 353 g m^{-2} $year^{-1}$. This was similar to the NAPP in the large wetland corrected for % plant cover ($\approx$ 380 g m^{-2} $year^{-1}$ on average; Table 4). The aboveground biomass estimated by regression in the first year of mesocosm wetlands was relatively low (121 g m^{-2} $year^{-1}$). The large wetland basin contained species other than *S. tabernaemontani* due to plant introduction in 1994. However, more than 90% of the total NAPP of the large wetland basin in both 1997 and 1998 was produced by *S. tabernaemontani*, the same species used in the mesocosms.

4. Discussion

We observed a number of differences between the large and mesocosm wetlands compared through this study (Table 5). These differences are discussed here.

4.1. Hydrology/hydraulics

Both the mesocosms and large wetland had similar HLR and hydraulic retention times (HRTs). Actual retention times for the large wetland might be overestimated because it was assumed that the entire volume of water in the wetland is involved in the flow. This is not always the case since mixing of the water was probably different in the two scales. It is more likely that there was less mixing and thus more short-circuiting of water due to basin morphology and topography in the large wetland. Retention time is a critical factor for nutrient retention in wetlands (Kadlec and Knight, 1996). The longer retention time of the large wetland in 1996 probably allowed the higher retention of nutrients observed relative to other years when similar yet much shorter retention time was observed in the large and mesocosm wetlands. Average velocities, while calculated and not directly measured at each scale, were similar for both scales. Turbulence is a physical factor that is clearly affected by scale. The small mesocosms have fetches of only 1 m or so while the large wetland can have a fetch of 150 m, causing considerable surface turbulence when wind is blowing parallel to the length of the wetland. This could explain some of the differences in parameters such as DO and redox in the different scales.

4.2. Physicochemistry and nutrient retention

Giddings and Eddlemon (1979) suggested 20–30% as a 'normal' CV range for microcosm variables simulating a large, field system. Kraufvelin (1998) pointed out that mesocosms with high variability may fail to simulate a large field system since their replicability is challenged by their 'soft' reality. Similar variability was observed between the large (CV = 20% on average) and mesocosm wetlands (CV = 16% on average) in inflow water chemistry parameters such as temperature, DO, pH, conductivity, and redox potential. However, inflow concentrations of N and P showed higher variability (CV = 84% on average) in the large wetland relative to mesocosms (CV = 31% on average). Higher variability of inflow nutrient concentrations in the large wetland may reflect other factors influencing the conditions of the variables in the system, such as flooding, which was not possibly simulated in the mesocosms. It seems that mesocosms maintained fairly high replicability while simulating the large wetland since the CV for most variables in the mesocosms was smaller than or similar to that of the large wetland for in/outflow.

Mesocosms showed a number of differences in water chemistry and nutrient change from inflow to outflow relative to the large wetland. The mesocosms were fully colonized with macrophytes in the second year, which did not allow much open space on the water surface. Extensive shading created by canopy cover on the water surface of the densely vegetated mesocosms caused both

Table 4
Estimated NAPP of macrophyte (mean ± S.E.) in the large wetland and mesocosms over a 2-year period

	Large wetland (10 000 m^2)		Mesocosm wetlands (1 m^2)	
	1997	1998	1997	1998
NAPP (g m^{-2} $year^{-1}$)	665 ± 52	729 ± 55	121 ± 11[a]	425 ± 33
c, correction factor [b]	~1.0	~1.0	~1.0	0.83
Corrected NAPP (g m^{-2} $year^{-1}$)	665 ± 52	729 ± 55	121 ± 11	353 ± 27
Plant cover (%)[c]	54	55	100	100
Effective NAPP (g m^{-2} $year^{-1}$)[d]	359 ± 28 a	400 ± 30 a	121 ± 11 b	353 ± 27 a

[a] Estimated by a regression between morphometric measurements and aboveground biomass harvested in 1998.

[b] c was $V_r/(V_r + V_e)$; a ratio of the volume of macrophyte attributed only to the area of mesocosm (V_r) to the total volume of macrophyte including the additional overhang over the sides of the mesocosms ($V_r + V_e$) in 1998, and assumed 1.0 for the other counterparts due to negligible overhang.

[c] Estimated by analysis of aerial photography for the large wetland. Mesocosms did not allow any open water space with 100% plant cover.

[d] Effective NAPP estimated by multiplying corrected NAPP by the percent plant cover in both types of wetlands. The same letters next to the values indicate no significance difference at $\alpha = 0.05$.

NAPP was estimated by harvesting peak biomass at the end of each growing season except for the mesocosms in 1997.

Table 5
Summary of characteristics of the two types of wetlands compared in the study over growing seasons

	Large-wetland	Mesocosm wetlands
Spatial scale	10 000 m^2	1 m^2
Source soil	Identical	Identical
Source water	Identical	Identical
Hydrology/Hydraulics		
HLR and HRT	Similar	Similar
Turbulence	Moderate to high	Low
Mixing	Moderate	Moderate to high
Macrophytes		
Effective NAPP	380 g m^{-2} $year^{-1}$	353 g m^{-2} $year^{-1}$
Percent cover	~55%	~100%
Species richness	Moderate	Low
Water quality change		
Temperature	Increase	Decrease
Dissolved oxygen	Increase	No change or decrease
PH	Increase	Increase
Conductivity	Decrease	Increase or no change
Redox potential	No change or decrease	Decrease
Nutrient retention capacity		
Total phosphorus	Moderate (fluctuating)	Low (decreasing)
Soluble reactive phosphorus	Similar (very high)	Similar (very high)
Nitrate plus nitrite	Similar (moderate to high)	Similar (moderate to high)
Ecosystem complexity		
Spatial heterogeneity	Moderate	Low to none
Biological complexity	Moderate to high (developing)	Low
Effective temporal scale	Long (years)	Short (weeks to months)

lower water temperatures and less light reaching the water surface. Less light caused lower primary productivity in the shallow water column and thus less DO and lower redox potential as observed. Rose and Crumpton (1996) reported a similar observation in which water temperature and DO were significantly lower in densely vegetated areas compared to the area of either sparse macrophytes or open water in a prairie pothole wetland. Moreover, significant surface turbulence, and thereby oxygen diffusion into and out of the water, was unlikely in our mesocosms. These more reduced conditions in the mesocosms compared to the large wetland may have subsequently influenced phosphorus transformations (Archer and Devol, 1992). Wetland sediments become anaerobic after they are flooded with water, so reduced conditions are the typical feature of wetlands (Mitsch and Gosselink, 2000). Reduced conditions influence phosphorus dynamics in anaerobic sediments by releasing back to the water inorganic phosphorus adsorbed with iron and aluminum oxyhydroxides (Patrick et al., 1973; Boström et al., 1982). This may be part of the explanation for the phosphorus export from the mesocosms in the second year when the DO and redox potential dropped significantly.

Chen et al. (1997) pointed out that periphyton growth on container walls in mesocosms must be considered when interpreting results from mesocosms since it could account for over 50% of total ecosystem gross primary productivity and biomass. Periphyton growth on the walls of our mesocosm wetlands, however, was negligible throughout this study. Light attenuation caused by the canopy cover of macrophytes in the mesocosms limited algal growth in the containers (e.g. Berg et al., 1999), resulting in relatively low water column productivity as indicated in drastic decrease in DO concentrations in the second year.

4.3. Macrophyte productivity

Mesocosms can distort important variables such as macrophyte productivity that may control the dynamics of large constructed wetlands (Busnardo et al., 1992; Boynton et al., 2001). Our study identified two scale artifacts that occur. When both were accounted for the NAPP both scales were the same. But they affected other functions of the wetland. One of the artifacts of small mesocosms observed in this study was macrophyte overhang; i.e., plant stems received sunlight from an area larger than that of the mesocosm in the second year. This artifact is due to a higher edge/area ratio of the mesocosm relative to the large wetland.

Another difference between mesocosms and large wetlands is the spatial patterns that result. Vegetation cover is essentially 100% in mesocosms because even one plant, with time, will fill the entire container. But on a large scale, it is rare to see a wetland with 100% vegetation cover for a number of reasons including depth variation, muskrat and goose herbivory, harvesting, and other disturbances. Our large wetland averaged 54–55% plant cover during our study. When percent cover is not used in calculation of effective NAPP, a plot of vegetation in our large wetland had a higher NAPP than a square meter of mesocosm. When areas that do not have vegetation are included, then NAPP is similar to that in the mesocosms. To say the vegetation is similar in productivity in the different scale ignores the fact that there is much open space in the large-scale wetland.

The net effect these two artifacts cause is a complete shading and to some degree protection for wind of the water column beneath the macrophytes in the mesocosms and more open space, exposure to wind turbulence, and much more water column productivity in the large wetland. Thus, ironically although the macrophyte NAPP calculates to be the same, major differences occur as a result of these artifacts. We would predict cooler temperatures, lower DO, higher conductivity, lower redox potential in the mesocosm wetlands and possible differences in nutrient uptake. In fact all of these effects were observed in this study.

4.4. Ecosystem complexity

Scale is defined broadly to include complexity of the system as well as space and time (Petersen et al., 1999). Fig. 4 shows conceptually the components and forcing functions of the two wetland systems compared in our study. Mesocosms are models of small patches of the large counterpart, and can only support a relatively small number of components. These are usually soil, water, macrophytes, and microbes. Our mesocosms, by their very nature, could not contain fish, waterfowl, muskrats, amphibians, wading birds, or other mobile animals. Some of these organisms are referred to as ‘ecosystem engineers’ (sensu Jones et al., 1994, 1997; Alper, 1998) and can exert major effects on ecosystem function. Wetland function is controlled not only by hydrology and nutrient inflows but also by biotic feedbacks from the biota (e.g. detrital buildup, transpiration, eatouts, sediment excavation, stream damming, etc.) (Mitsch and Gosselink, 2000). Differences in complexity between scales can have dramatic effects on biogeochemical functions of the system, including biogeochemical pathways as illustrated in Fig. 4.

Adey et al. (1996) argued, however, 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 which support a specific functioning (i.e., phosphorus retention) of the system studied. Our mesocosm wetlands contained the same relative forcing functions (sunlight, water and nutrient inflow) and main components (plants, sediments and water) as those in the large wetland that allowed self-organization of the system to manifest itself, thus simulating a large wetland for their macrophyte production and nutrient retention capacity over a relatively short period of time (Table 5). In that sense, the mesocosms do offer a reasonable model of the large system in the temporal scale even without all of the complexity.

4.5. Scale considerations of mesocosm experiments

We noticed anomalies of mesocosms in the second year that may affect interpretation of results for wetlands in general. In that case, mesocosm research can be elegant in its replication and statistical power but the findings can simply be wrong in interpreting how wetlands work. Some of the scale effects in the mesocosms in the second year were 100% plant cover and extensive shading, decreases in redox, rapidly decreasing phosphorus retention, and macrophyte overhang. We believe that it is not readily possible to simulate all realistic physical and biological conditions and the interactions of both in mesocosms (e.g., water mixing, turbulence at the sediment-water interface of the large wetland) due to their small sizes and boundary conditions (wall effects).

Comparison of the two scales of wetland systems in our study was not natural system versus artificial system. Both systems were supported by

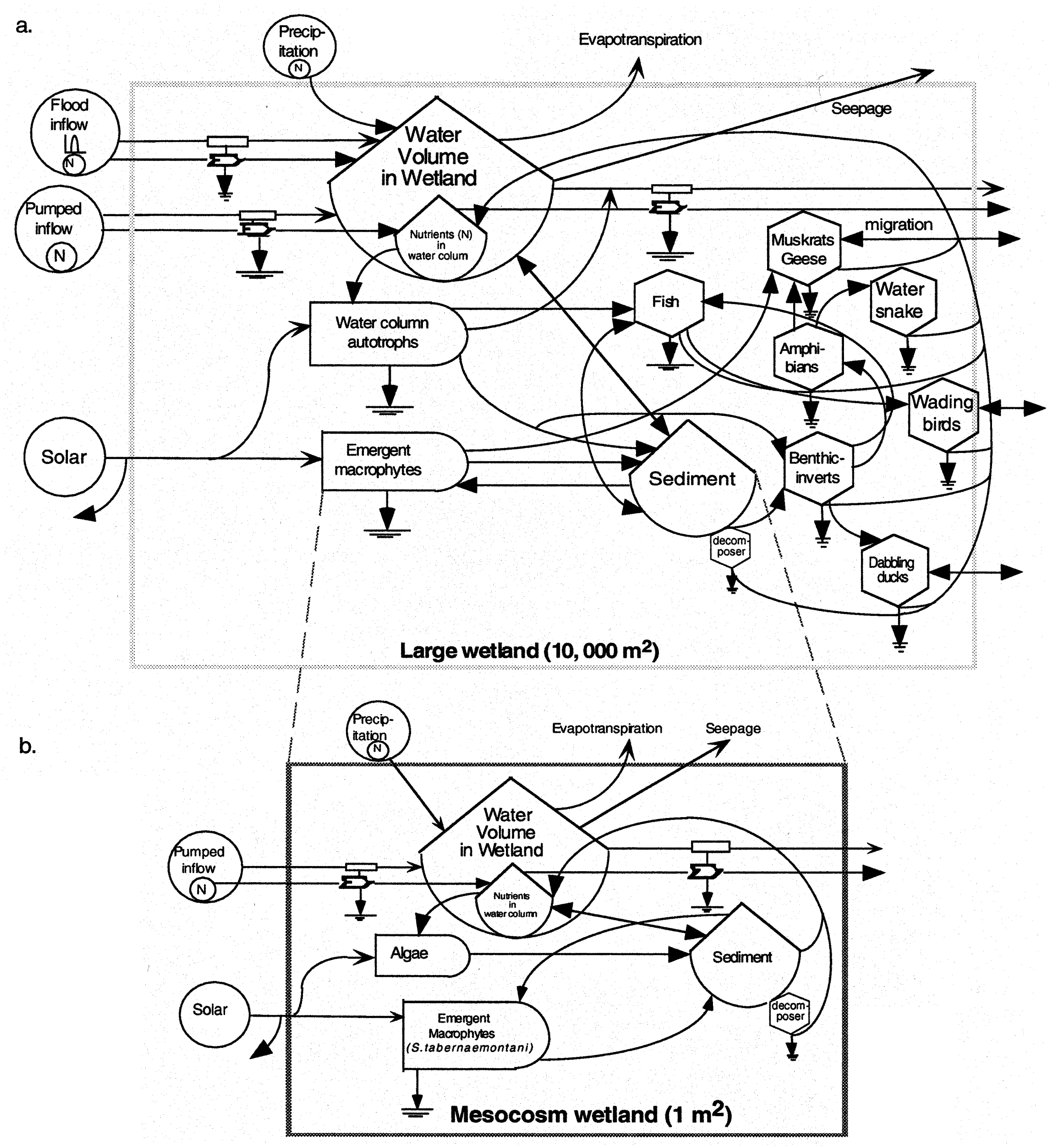

Fig. 4. Conceptual model of two experimental wetlands showing biocomplexity scales compared in this study (a) large scale, (b) mesocosm scale. Model also illustrates processes involved in phosphorus retention by these two types of wetlands. Thicker boundary line of mesocosm symbolizes the container.

artificially maintained hydrology (pumps, gravity flow), yet both developed naturally with no other human intervention. In terms of system performance for particular functions, the mesocosms provided replicated measurements with the resulting statistical power of basic ecosystem processes that can be studied over a reasonably 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. Many previously conducted mesocosm experiments have failed to report exact spatio-temporal scales used (Petersen et al., 1999). Lack of care concerning the scale at which the experiments are conducted may cause poor data interpretation and conclusions of mesocosm results. Adey and Loveland (1991) recommend that mesocosm artifacts be noted for successful mesocosm design. We agree and recommend that study of size effects of mesocosms continue through multi-scale experimental design or scale comparisons. Otherwise, it is a question of statistically rigorous studies that may have little reality.

4.6. Temporal scale

It seems reasonable to limit the use of wetland mesocosms for the study of specific biogeochemical processes to a period of no more than 2 years. Extensive 'pot-bound' vegetation growth and premature low redox conditions can make results after 2 years questionable. Our experience with several wetland mesocosm studies (e.g. Ahn et al. 2001; Svengsouk and Mitsch, 2001; this study) support that general guideline. 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. We need to consider the duration of mesocosm experiments based on the size of system used in the study and make an effort to determine quantitative scaling relationships between size and time period.

5. Conclusions

The study was conducted to explore the effects of experimental scale on ecological functions in wetlands and to identify positive and negative aspects of using mesocosms in simulating real field-scale wetlands. The mesocosms provided a certain reality by simulating a large wetland for the study of water quality and perhaps early vegetation succession functions of created wetlands. The outcomes of our study, however, showed some limitations of mesocosms and suggested that we consider experimental size, time, and artifacts of mesocosms used before results from mesocosm studies are generalized to large wetlands. There were other factors or components not included in the mesocosms such as large animals, realistic hydraulic conditions, and flooding effects etc., making it difficult to attribute the differences between our mesocosms and the large wetland only to size. The differences found might be looked upon as being due to wetland 'type'.

Mesocosms allow replicability and repeatability of experiments at a much lower cost than do large, field ecosystems. Practical constraints such as cost, availability of equipment, and land availability are also more likely to determine system size and experimental duration in many cases of ecological research. Investigating and reporting the artifacts of mesocosms and any difference between the studies conducted at different scales will contribute to better design and interpretation of mesocosm experiments on wetland functions.

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