Arboretum Leaflets
Restoration Discovery Research

Mesocosms: An idea that became a reality and then a necessity!

My idea to remodel a fallow pine tree nursery for research using mesocosms led the Arboretum Committee to designate about ¼ acre for such a facility. Using mid-sized experimental containers (and their smaller cousins, microcosms), we were able to control factors like water level and nutrients and species composition, and thus determine cause→effect, not just correlation.

"Mesocosm" means intermediate-size containers that are bigger than microcosms, like flower pots, and smaller than macrocosms, like ponds. A mesocosm facility requires a fenced-in area to exclude deer and other "vandals," a water supply, electricity, a large gate to allow a truck to deliver soil and sand, and space for tanks and buckets. Maintenance is minimal, except for weed control.

Now, after 17 years of use involving >1000 meso- and microcosms, the Mesocosm Facility has proven its worth in serving research needs for:

- 6 PhD dissertations (Roberto Lindig-Cisneros, Suzanne Kercher, Andrea Herr-Turoff, Aaron Boers, Beth Lawrence, Jim Doherty),
- 4 MS theses (Cristina Bonilla-Warford, Rachel Miller, Debbie Maurer, Sally Gallagher),
- 1 postdoctoral study (Tracy Rittenhouse),
- >20 peer-reviewed papers, and
- Numerous mentored-undergraduates, at least two of whom now have their own PhDs (Hannah Kinmonth and Steven Hall).

It all began in **1998**: **Roberto Lindig-Cisneros** set up 48 mesocosms to test factors that allow sedge meadows to resist weed invasions. Roberto managed the vegetation, but makeshift snow fencing couldn't keep out nocturnal marauders. Not until animals began digging up our precious experimental replicates did we finally gain administrative approval to install a fence. Then, in a day, an 8-foot high chain link fence transformed the area into a facility that excluded deer and announced that research is worth protecting.

Roberto planted 48 mesocosms with fowl manna grass (*Glyceria striata*) plus 1, 6, or 15 native species. To our surprise, reed canary grass (*Phalaris arundinacea*) was unable to establish from seed until Roberto cut small gaps in each canopy. Then, the 1- & 6-species canopies allowed reed canary grass to establish about twice as many seedlings as in the denser 15-species canopies. Given moist soil, complex canopies limit seed germination by capturing much of the light. Where conditions were favorable for native plants, dense canopies inhibited weed invasion.

Roberto Lindig-Cisneros tending our first mesocosm experiment, set up in 1998.

Lindig-Cisneros, R. and J. B. Zedler. 2002. *Phalaris arundinacea* L. seedling establishment: Effects of canopy complexity in fen, mesocosm and restoration experiments. Canadian Journal of Botany 80:617-624.

Lindig-Cisneros, R. and J. B. Zedler. 2002. Relationships between canopy complexity and germination microsites for *Phalaris arundinacea* L. Oecologia 133:159-167.

Where is Roberto now? Dr. Lindig-Cisneros is Professor of Ecology at Universidad Nacional Autónoma Mexico – Morelia, where he created his own mesocosm facility. Roberto continues to develop innovations in ecosystem restoration, combining native species and ecosystem services (such as forest plantations to reduce erosion and using native legumes to supply nitrogen to lava soils). He established mesocosms to control variables in several restoration experiments.

2000: **Debbie Maurer** extended Roberto's study to field and greenhouse experiments, then wrote up the summary of several studies for practitioners in *Ecological Restoration.* In the greenhouse experiments, both flooding and heavy shade decreased reed canary grass shoot biomass, but when an adult plant was present, new shoots were subsidized. With parental help, offshoots grew faster and further into dense canopies. Rapid expansion by this invader is explained by a clonal subsidy, morphological plasticity, and nutrient availability. Where nutrients are plentiful, it grows taller than the natives and captures more light; where nutrients are scarce, it expands belowground to forage for more nutrients.

Maurer, D. A., and J. B. Zedler. 2002. Differential invasion of a wetland grass explained by tests of nutrients and light availability on establishment and vegetative growth. Oecologia 131:279- 288.

Maurer, D. A., R. Lindig-Cisneros, K. J. Werner, S. Kercher, R. Miller, and J. B. Zedler. 2003. The replacement of wetland vegetation by *Phalaris arundinacea* (reed canary grass). Ecological Restoration 21:116-119.

Where is Debbie now? Ms. Maurer is the Manager of Ecological Restoration for Lake County Forest Preserve District, Illinois. She manages a staff of ecologists and wildlife biologists and develops large restoration projects, field research, and partnerships.

1999: **Cristina Bonilla-Warford** grew prairie cordgrass (*Spartina pectinata*) in 140 5-gallon pots (we called them microcosms) to test this species' potential for use in stormwater wetlands. We wanted to find an alternative to invasive reed canary grass. Prairie cordgrass surprised us by growing vigorously in all treatments, namely, with 24-hr flooding weekly in early summer, weekly in late summer, every three weeks all summer, weekly all summer, and with no flooding. Neither timing nor frequency of flooding affected total stem length or shoot biomass. Knowing its broad flood tolerance, we recommended cordgrass for further testing in stormwater wetlands, along with early planting of *Glyceria striata* (a native grass) to reduce weed invasions.

Bonilla-Warford, C., and J. B. Zedler. 2002. Potential for using native plant species in stormwater wetlands. Environmental Management 29:385-393.

Where is Cristina now? I've lost track, but her first positions involved education at public gardens in Chicago.

2000: **Rebecca Miller** grew reed canary grass in 120 microcosms to see how eight hydroperiods might explain its dominance compared to prairie cordgrass. When grown alone, shoot biomass was similar for the two species, but the light-weight stems of reed canary grass produced twice the stem length of cordgrass. Reed canary grass grew best when wetter and drier conditions alternated weekly, while cordgrass grew best with prolonged (4-week) flooding. The reed canary grass surprised us by changing its morphology when grown with cordgrass. It increased its total shoot length:biomass ratio by 50%! We concluded that reed canary grass was able to dominate wetlands by producing far more total shoot length per unit biomass and by having adaptable morphology. (This finding led to Herr-Turoff's study of morphological plasticity, below).

Miller, R. C., and J. B. Zedler. 2003. Responses of native and invasive wetland plants to hydroperiod and water depth. Plant Ecology 167:57-69.

Where is Becky now? After obtaining her degree, she emigrated into Library Science and a job in eastern US.

2000: **Suzanne Kercher** grew 17 wetland taxa in 340 microcosms (1-gallon pots each inside its own bucket) to compare their morphological traits and growth under four hydroperiods: constant drawdown, cyclic flooding and drawdown, cyclic flooding and drought, and constant flooding for 10 weeks. She found that reed canary grass and broadleaf cattail (*Typha latifolia*) responded similarly by outgrowing the other perennial species in all four hydroperiods. Also, reed canary grass had the most root airspace, and the grasses and graminoids nearly always tolerated flooding better than forbs, perhaps by incorporating more root airspace. The least flood-tolerant species grew best in drier, lower-nutrient conditions. We hypothesized that reed canary grass and cattail would dominate under a variety of hydrologic conditions where nutrients are abundant, as in urban and agricultural landscapes.

Kercher, S. M., and J. B. Zedler. 2004. Flood tolerance in wetland angiosperms: a comparison of invasive and noninvasive species. Aquatic Botany 80:89-102.

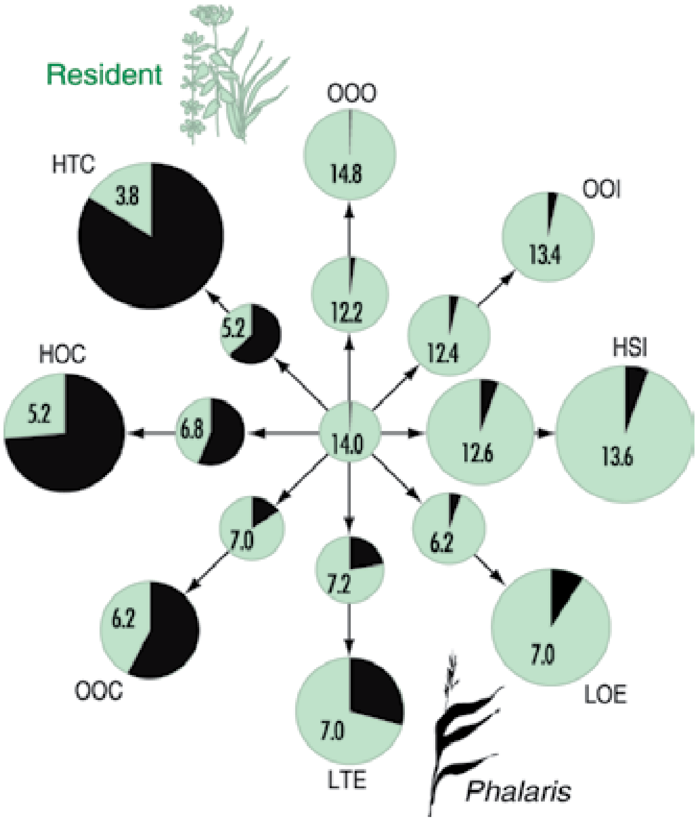
2001: Next, Suzanne Kercher (and many helpers) set up 160 new, tall mesocosms (95 cm, surface area ~1.1 m^2) with 14 wet-prairie species per mesocosm to determine which conditions promote invasion by reed canary grass. After allowing the native species to establish, Suzanne introduced just 4 reed canary grass seedlings to each mesocosm. She initiated 27 treatments in June 2002, varying nutrient additions, sediment additions, and flooding (3 levels of each). Species richness decreased with sediment addition (especially nutrient-rich topsoil) and/or flooding for $\geq$4 weeks. As natives died, up to 4 times as much light was transmitted through the canopy. Light availability in July and September was a strong predictor of reed canary grass growth. Nutrients further increased productivity. A separate experiment revealed a synergism between nutrients and simulated grazing. Results led us to advise that multiple factors be mitigated simultaneously to reduce invasion of this tall, clonal, aggressive grass.

Zedler, J. B., and S. Kercher. 2004. Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences 23:431-452.

Kercher, S. M., and J. B. Zedler. 2004. Multiple disturbances accelerate invasion of reed canary grass (*Phalaris arundinacea* L.) in a mesocosm study. Oecologia 138:455-464.

Zedler, J. B., and S. Kercher. 2005. Wetland resources: Status, ecosystem services, degradation, and restorability. Annual Review of Environment and Resources 30:39-74. Annual Reviews, Palo Alto, CA.

Where is Suzanne now? After teaching environmental science at Columbia College in Missouri, Dr. Kercher shifted to teaching high school full-time—an opportunity to engage the next generation in ecological thinking.



The number of resident species declined from 14.0 with no additions (000) to 3.8, where reed canary grass was most productive with High nutrients + Topsoil + Constant flooding (HTC). Each ring of pie charts represents a year of outcomes in 8 of the 27 treatments. See Leaflet 8.

2002: **Andrea Herr-Turoff** and Suzanne Kercher followed the invasion of reed canary grass into wet meadow vegetation over the two-year experiment. The invader produced the most biomass in treatments with either nutrient addition, flooding, or both. Native species were outcompeted where disturbance (nutrients, floods, sediments) acted alone and in combination to make the resident wetland community more invasible and the invader more aggressive, leading to monospecific stands.

Andrea also set up microcosms to test competitive interactions among reed canary grass, prairie cordgrass, and Canada bluejoint (*Calamatrostis canadensis)* grown in combination and with varied nitrogen additions. To make the root biomass easier to separate from the soil, she grew the plants in sand. [Clay is notoriously hard to separate from fine roots.] However, that led to a surprise: All plants grew so slowly that she could not document any interactions among species. On the positive side, we had found a condition that reed canary grass could not monopolize! Perhaps this explains why reed canary grass is not so common in Wisconsin's central sand plains.

Andrea made additional critical discoveries by taking detailed measurements of reed canary grass as it continued to dominate the mesocosms. She found that reed canary grass was "plastic" in its morphology—it could form tussocks under continuous flooding and swards under well-drained conditions! Best of all was her news that the invader was no better at retaining nitrogen than native plants, which allowed scientists from the Wisconsin Dept. of Natural Resources to recommend against using reed canary grass in wetlands designed to remove nutrients (treatment wetlands). Research results led directly to policy!

Herr-Turoff, A., and J. B. Zedler. 2005. Does wet prairie vegetation retain more nitrogen with or without *Phalaris* invasion. Plant and Soil 277:19-34.

Kercher, S. M., A. Herr-Turoff, and J B. Zedler. 2007. Understanding invasion as a process: The case of *Phalaris arundinacea* in wet prairies. Biological Invasions 9:657-665.

Herr-Turoff, A. and J. B. Zedler. 2007. Does morphological plasticity of the *Phalaris arundinacea* canopy increase invasiveness? Plant Ecology 193:265-277.t

Where is Andrea now? Until recently, Dr. Herr-Turoff was our Student Coordinator in the UW Botany Department, using her ability to manage large data sets and tracking detailed information. Her administration of the Ecological Restoration (non-thesis track) within the Botany MS program was critical to launching the careers of many graduate students who gained the skills needed to practice restoration. Andrea moved to Pennsylvania to join her father and her college-student daughters.

2004: **Aaron Boers** set up a mesocosm experiment and 72 microcosms to test the hypothesis that stabilizing water levels enhances the spread of hybrid cattails (*Typha* x *glauca*). Indeed, constant inundation allowed cattails to produce 56% more biomass than a water regime with two drawdowns. Why did that happen? Plants under constant inundation accumulated more phosphorus (P) with longer hydroperiods. The results demonstrated that P becomes soluble and available to cattails when soil loses oxygen—a process called internal eutrophication or internal loading. This explains why a dam that stabilizes water level favors cattails behind that dam. Designers of stormwater ponds should take heed—P that is predicted to be stored in the sediment can be re-mobilized by cattails in shallow water.

Boers, A., C. Frieswyk, J. Verhoeven and J. Zedler. 2006. Chapter 10: Contrasting approaches to the restoration of diverse vegetation in herbaceous wetlands. Pp. 225-246 in R. Bobbink, B. Beltman, J J.T.A. Verhoeven, and D.F. Whigham, eds. Wetlands as a natural resource, Vol. 2. Wetlands: Functioning, Biodiversity Conservation and Restoration. Springer Verlag.

Boers, A. M., and J. B. Zedler. 2008. Stabilized water levels and *Typha* invasiveness. Wetlands 28: 676-685.

Where is Aaron now? Dr. Boers recently became the Restoration Ecologist at Resource Environmental Solutions. He identifies and evaluates sites for habitat restoration to be used as mitigation for unavoidable impacts to wetlands and streams. He designs wetland and stream restoration projects and prepares mitigation plans for approval by resource agencies.

One tussock was harvested before this photo was taken.

2006: **Beth Lawrence** and I set up an experiment to test for differences in tussock sedge (*Carex stricta*) growth and tussock formation among six hydroperiods. We began with 12 replicates per hydroperiod using young seedlings, and Beth added a test of nutrient loading on tussock formation in years 2007 and 2008. Inundation accelerated tussock formation, and N+P additions increased overall productivity. I was surprised to see that, within two growing seasons, continuous flooding led to loosely-formed tussocks averaging 10 cm tall (with one that was 17 cm tall!). With constant low water, tussock sedge formed only short mounds (~2 cm). More water → more microtopography! After three growing seasons, tussocks were predominantly organic (74–94% of dry mass) and composed of leaf bases (up to 59%), fine roots (up to 31%), and duff. Only the plants subjected to high water produced an abundance of vertical rhizomes and shoot bases as in field-collected tussocks. We concluded that prolonged hydroperiods accelerate tussock formation, which could restore wetland microtopography and associated functions, including carbon accumulation.

Lawrence, B. A., and J. B. Zedler. 2011. Formation of tussocks in sedges: effects of hydroperiod and nutrients. Ecological Applications 21: 1745-1759.

Lawrence, B. A., and Zedler, J. B. 2013. Tussock structural composition and carbon storage in *Carex stricta* sedge meadows. Wetlands. Online.

Lawrence, B., T. Fahey, and J. B. Zedler. 2013. Root dynamics of *Carex stricta*-dominated tussock meadows. Plant and Soil 364:325-339.

Where is Beth now? Dr. Lawrence is an Assistant Professor in the Dept. of Environmental Science at DePaul University. She is an applied plant ecologist who works to

2006: What next? It was time to remodel the tall mesocosms for new research. I found a Bobcat operator to help, beginning by dumping the contents of all 160 tall mesocosms. Tubs full of sediment are far too heavy to empty by hand. I ordered well-mixed sand and topsoil from a local supplier and found volunteers to help refill 72 tubs in an 8x9 array. Like a dance, volunteers moved 8 tubs to form the first row. Then the Bobcat operator dumped a bucket load of sand into each tub, which volunteers leveled and tamped with rakes. When the first row had its bottom layer of sand, it was time to add the topsoil. With the first row complete, we could proceed to the next row, which cut off access to the first row. That's why the work had to be choreographed. Nine rows of eight tubs = 72 mesocosms. It was a busy, productive day! This photo shows the same process underway in 2010.

enhance the understanding and management of natural ecosystems. She is currently engaged in field, greenhouse, and laboratory research exploring wetland plant invasion and greenhouse gas emissions, carbon cycling in restored tallgrass prairie, and how vegetation structure influences urban wildlife.

2008: **Sally Gallagher** grew tussock sedge in microcosms to determine how best to propagate this wetland plant for restoration purposes. The addition of nitrogen increased total biomass of 15-month-old plugs, especially belowground, resulting in root:shoot biomass ratios >1.0. With inundation, plugs shifted more biomass to shoots, and with good drainage, more to roots. High nitrogen and water levels at the soil surface maximized rhizome production. Thus, tussock sedge was plastic in its root:shoot ratio. By varying N and water level, growers and restorationists could tailor seedlings and plugs for use in a varied restoration sites, potentially increasing transplant establishment and survival.

Gallagher, Sally K. 2009. Use of nitrogen and water treatments to manipulate *Carex stricta* Lam. Propagules. M.S. Thesis, University of Wisconsin-Madison. See also Leaflet 22.

Where is Sally now? Ms. Gallagher works for Wisconsin DNR, where she evaluates the progress of wetlands that are restored as mitigation for permitted projects.

2008 Dr. **Tracy Rittenhouse**, a Postdoctoral Fellow, scrubbed up 36 of the empty, tall mesocosms, filled them with well water, and tested the hypothesis that the invasive reed canary grass (which can contain toxic alkaloids) would reduce survival, growth, and development rates of four tadpole species. To her surprise, neither American toads (*Anaxyrus americanus*), Cope's gray treefrogs (*Hyla chrysoscelis),* pickerel frogs (*Lithobates palustris*), nor wood frogs (*Lithobates sylvatica*) grew differently than when fed a

Jim Doherty in front of 72 tussock sedge mesocosms

mixture of native grasses. It was the quantity of food, not its quality that influenced tadpole performance.

Rittenhouse, Tracy. 2011. Anuran larval habitat quality when reed canary grass is present in wetlands. Journal of Herpetology 45(4):491-496. For more about the importance of frogs, see Leaflet 35.

Where is Tracy now? Dr. Rittenhouse is a professor in the Department of Natural Resources and the Environment at the U. of Connecticut, where she recently set up her own a mesocosm facility (it's contagious).

2010: **Jim Doherty** and I wanted to test the idea that restoration ecologists could increase ecosystem function (diversity and productivity) simply by planting more species. Ecologists call this biodiversity-ecosystem function (BEF) theory. So, when we could not conduct the BEF test in Arboretum swales*, we set up 36 tall mesocosms with sand and topsoil, as usual. We planted 9 plugs per mesocosm, as either 1, 3 or 9 species, chosen at random from 21 native wetland species. Contrary to theory, plant diversity and productivity were uncorrelated. Tall productive graminoids increased aboveground biomass and had few co-occurring species. BEF theory was rejected for wetlands where productive dominants tended to suppress diversity.

*The mesocosm facility rescued a research project that promised to test these plantings in three wetland swales. Because contractors either planted seed that was nonviable or mishandled the seed, the swales were bare and attractive to cattails and other weeds. The contract did not require seeds to germinate (!) so we resorted to "Plan B," a mesocosm experiment.

Doherty, J. M., and J. B. Zedler. 2014. Dominant graminoids support restoration of productivity but not diversity in urban wetlands. Ecological Engineering 65:101-111. For more about the swales study, see Leaflests 27-28.

Where is Jim now? Dr. Doherty recently accepted a position at Stanford University, which operates an online high school and college prep program for gifted students. He is happily developing his teaching skills in chemistry and environmental science courses.

Winter 2013-14: Dr. **Jon Pauli**, Assistant Professor in the Forest & Wildlife Ecology Dept., simulated climate warming at the soil-snow surface (the subnivium) in a greenhouse that trapped partial snowfall. Despite simulating a warmer winter, he reported colder minima, which could threaten sensitive biota that overwinter in the subnivium.

Petty, S.K., B. Zuckerberg and J.N. Pauli. *in press*. Winter conditions and land cover structure the subnivium, a seasonal refuge beneath the snow. PLOS ONE.

Jiangxiao Qiu measuring temperature and soil moisture. Photos courtesy of J. Qiu.

What next? Thanks to their pilot study at the Arboretum, Pauli and Petty are now funded to explore regional effects of altered snow cover at 9 sites from southern Wisconsin to Michigan's Upper Peninsula.

2014: A total of 66 microcosms set up by **Jiangxiou Qiu** and Dr. Monica Turner (Zoology Dept.) revealed factors that influence how an invasive worm affects carbon dynamics by modifying understory litter and soil; preliminary results are that the "crazy jumping worm" reduces the litter layer and changes both physical and chemical properties of forest and prairie soils (dissertation anticipated in 2016).

2015: A dream come true: The mesocosms are now indispensible. Two students recently chose projects to improve sedge meadow restoration. MS student **Chris Hirsch** is testing a grass-specific herbicide to see if he can remove reed canary grass from several invaded mesocosms without harming tussock sedge. Meanwhile, **Leah Weston** is determining how tussock sedge is affected by road salt and nitrogen (as in urban runoff) for her Botany senior thesis. Physiologist colleagues, Dr. Kate McCulloh (UW Botany) and Dr. Scott Holaday (Texas Tech), are helping us with methods to assess plant stress.

The mesocosms facilitate research and researchers help sustain the mesocosm facility.

Compiled by Joy Zedler from published papers
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