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Plant community establishment in a restored wetland: Effects of soil removal

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Abstract

Question: This study investigated the establishment of wetland plant assemblages following soil removal and restored hydrology in a former agricultural field. The following questions were posed. Does plant community composition differ as a result of soil removal? Does soil removal reduce the frequency of non-wetland plants? Does soil removal reduce the frequency of non-native invasive plants?

Location: The Panzner Wetland Wildlife Reserve (PWWR) in Summit County, northeastern Ohio, USA.

Methods: During 2000-2001, restoration was conducted on two adjoining fields (3.9 ha total) by excavating the upper 40-50 cm of soil layer and establishing 12 10 m × 10 m undisturbed control plots. Preliminary data included seed bank composition and soil organic matter, estimated from three different soil depths on the control plots. In spring 2004, a 10 m × 10 m soil-removed plot was established adjacent to each control plot. Plant percent cover of all species was estimated within the center 5 m × 5 m of every plot. Above-ground biomass of all species from three 0.25-m^2 quadrats was collected. Environmental water measurements included water depth, temperature, dissolved oxygen, pH, and conductivity.

Results: The top 10 cm of soil contained the most seeds, the highest species diversity, the greatest proportion of annual to perennial plants, and the lowest organic content. Obligate and facultative wetland plants were found in soil-removed plots while facultative upland and upland plants were found in control plots. The only plots with arable weeds were the control plots. However, plant communities on soil-removed plots in the North field, which had a higher elevation (ca. 15-20 cm), had a different species composition than soil-removed plots in the South field.

Conclusions: The results of a controlled, replicated large-scale study on the effects of soil removal showed that soil removal altered both the biotic and abiotic environment, but that the proximity to the water table was the primary controlling factor in the assembly of plant communities.

Keywords: Assembly rule; CCA; Field-study, Hydrology; Invasive species; Peatland; Restoration.

Introduction

Over the last two centuries, many North American wetlands have been impacted by human development, pollution and the spread of invasive species (Tiner 1984; Dahl 1990, 2000; Kentula 1996; Fraser & Keddy 2005). In the United States, 53% of all historical wetlands in the lower 48 states and over 90% of Ohio's wetlands have been destroyed by anthropogenic causes (Dahl 1990; Little & Waldron 1996). The conversion of wetlands for agriculture is the predominant reason for loss of wetland habitat (Dahl 2000).

Although wetland restoration is a common practice, studies have found that many mitigation wetlands lack ecological functions provided by natural habitats (Zedler 1993; Kentula 1996; Galliguh & Rogner 1998). For example, a study of 168 mitigation wetlands in the Midwest and Florida found that only 15% of the mitigated wetlands were fully successful (Galliguh & Rogner 1998). Efforts to improve success of wetland reconstruction projects require an understanding of the environmental factors that determine resulting plant and animal community structure.

Hydrology is often considered the most important factor that influences wetland flora (Mitsch & Gosselink 2000), because wetland plants are adapted to specific hydrological regimes (van der Valk et al. 1994; Baldwin et al. 2001). Many wetland species can tolerate periodic flooding, but long-term flooding, especially of seedlings, can reduce their growth and survivorship (Kercher & Zedler 2004; Fraser & Karnezis 2005). Therefore, successful restoration projects often must first restore a wetland's hydrology (Hammer 1996).

The purpose of our study was to investigate the establishment of wetland plant assemblages following soil removal and restoration of hydrology in a former agricultural field. Soil removal is used in wetland restoration projects on former agricultural land because it can: (1) remove residual weeds from the seed bank (Dalrymple et al. 2003; Zedler & Kercher 2004); (2)

remove persistent pesticides and fertilizers (Marrs 1993; Jacquemart et al. 2003); and (3) restore a natural wetland hydrology (Pfadenhauer & Grootjans 1999; Verhagen et al. 2001; Dalrymple et al. 2003; Jacquemart et al. 2003).

This technique has been applied to agricultural lands that were formerly heathland (Verhagen et al. 2001; Jacquemart et al. 2003; van den Berg et al. 2003), salt marshes (Bakker et al. 2002), wet dune slacks (Jungerius et al. 1995; Bakker et al. 2005), and wet meadows (Dalrymple et al. 2003; Hölzel & Otte 2004). Soil removal can be expensive in large restoration projects; therefore, understanding the limitations and merits of soil removal will have useful management implications.

Despite widespread use of soil removal in wetland restoration, there are few large-scale (> 10 m^2), long-term, controlled studies that measure its impact on ecological factors that affect wetland community structure (Jacquemart et al. 2003). This study takes an applied approach to compare plant assemblages in areas that had soil removed with unmanipulated areas. We tested the following hypotheses:

1. A greater abundance and diversity of seeds, including arable weed species, will occur in the upper soil strata. Therefore, soil removal will reduce the relative abundance of arable weeds in the plant community compared to the control plots.
2. Soil removal will reduce the soil nutrient pool with the result that the biomass of vegetation grown in soil-removed plots will be less than control plots.
3. Soil removal and the concomitant changes in hydrology, seed bank, and soil nutrients will impact plant community composition and promote more flood tolerant plants (i.e. obligate wetland species) in soil-removed plots than control plots.

Methods

Study site description

The study site was located on the Panzner Wetland Wildlife Reserve (PWWR) in northeastern Ohio (Summit County), which contains ca. 38 ha of restored wetlands. The PWWR property, originally a forested peatland, was drained and cleared for agriculture in 1938. The soils are hydric Carlisle muck (Cg) and Olmsted loam (Od) with peat deposits ranging from one to several meters thick (S. Panzner, PWWR, pers. comm.). Continuous drainage using mechanical pumps, a network of ditches, and subsurface drainage tiles were needed to farm crops such as celery, lettuce and onions. Farming practices ceased when restoration efforts were initiated in 2000.

Experimental design

We selected a pair of adjoining fields (total area 3.9 ha), henceforth termed the North field and South field. The two fields were contiguous but the North field was about 15-20 cm higher in elevation than the South field.

In 2000, 12 10 m × 10 m control plots were established; six plots in the North field and six plots in the South field. The soil and existing plant communities were not disturbed within these plots during the study. In the surrounding field outside the control plots, 40-50 cm of upper soil surface was removed with bulldozers. Excavation of each field took several months, beginning with the North field in 2000 and ending in the South field in 2001. In addition, mechanical pumps and drainage tiles were removed. All sources and amounts of water inputs (e.g. precipitation, groundwater and surface water) were similar for both fields but due to the elevation difference the South field was more deeply flooded than the North field. In 2004, 12 10 m × 10 m treatment plots (i.e. the soil-removed plots) were randomly established at one of the four cardinal compass points adjacent to and separated by a 5-m buffer from each control plot.

Most of the plants colonized from the existing seed banks and by dispersal from nearby wetlands and uplands. However, the North field was seeded one time in 2000 after excavation with ca. 2.3 kg of a seed mix of 32 wetland plant species from the Ernst Conservation Seeds, Inc (Meadville, Pennsylvania) (App. 1). The South field was also seeded one time in 2001 with ca. 3.2 kg of a similar seed mix of 29 species that were collected from the PWWR property (App. 1).

Biotic and abiotic sampling

In 1999, the soil seed bank was sampled before wetland restoration commenced. At each of five locations spread across the PWWR, three replicate 10 cm^3 soil samples at three depths (0-10 cm, 10-20 cm and 20-30 cm) were collected. Samples were spread out on trays (40 cm × 15 cm) to a depth of ca. 3 cm, and provided with a 16-h photoperiod and 20 °C constant temperature in a controlled greenhouse (Leck et al. 1989). All germinated seedlings were counted and identified to species or genus.

In 2000, soil samples were collected to measure percent organic matter. Pits were hand-dug at the edge of each control plot and soil cores (15 cm diameter) were used to collect undisturbed soil at three depths (0-20 cm, 21-40 cm, and 41-60 cm) at the edge of the pits. Percent organic matter of the peat was estimated by measuring the loss on ignition after burning soil samples in an oven at 550 ºC for 2 h (Blume et al. 1990).

In July 2004, four years following the experimental manipulation, plant assemblages were sampled in the soil-removed and control plots. The center 5 m × 5 m area of each plot was marked off and plant percent cover was visually estimated for all species in this area. Aboveground biomass was sampled in three randomly located 0.5 m^2 quadrats in each 5 m × 5 m area. In each quadrat, all plants were clipped at the soil surface, separated by species, and placed in paper bags. In flooded quadrats, all submersed or floating plant species (e.g., *Ceratophyllum*, *Lemna*) were removed with a sieve and placed into plastic bags. All plant samples were held in a 4 ºC refrigerator for 2-4 weeks until processed. In the laboratory, aquatic plants were rinsed clean of debris. All plants were dried at 68 °C for 48 - 62 h to a constant dry weight. Plants were cooled to room temperature in a desiccating chamber (2-4% relative humidity), and dry weight biomass was measured to 0.0001 g on an electronic balance (Mettler Toledo AG204, PG5002-S). Vouchers of all species were collected to confirm field identifications, and deposited in the Kent State University herbarium. All vascular species were grouped by their wetland categories whenever appropriate (Reed 1988; Andreas et al. 2004). The wetland categories describe each species' typical habitat and are as follows: UPL (upland), FACU (facultative upland), FAC (facultative), FACW (facultative wetland) and OBL (obligate wetland). Species with a ± specification were grouped in the primary category (i.e. FACW+ was classified as FACW).

In July 2004, water level meters were installed in the center of each soil-removed and control plot to measure ground water levels. Water level meters were constructed from 5 cm diameter PVC pipe with holes drilled in the lower 30-40 cm to allow for ground water infiltration. In August 2004, we measured depth to water table in each water level meter with a measuring tape. In addition, water pH, conductivity, dissolved oxygen and temperature were measured in each water level meter using field meters (Model 85-YSI; Cole Palmer, PhTester).

Statistical analysis

Biotic analyses included Shannon-Wiener Diversity Indices (Zar 1984), species richness, total biomass, and percent cover. The abiotic analyses included soil percent organic matter, depth to water table, pH, conductivity, dissolved oxygen and water temperature. All data were analysed with a 2-way fixed-effect ANOVA, with field (North and South) and treatment (soil-removed vs. control treatments) or field (North and South) and strata (0-20 cm, 21-40 cm, 41-60 cm) the factor variables. When Field × Treatment interactions were significant (i.e. $P < 0.05$), *post hoc* contrasts were performed to detect differences using JMP (Anon. 1999).

Plant community structure was analysed with ordination using canonical correspondence analysis (CCA) (McCune & Medford 1999) using percent cover data. Although we also ran canonical correspondence analyses with biomass data, the results were similar to the percent cover data and therefore are not included in this paper.

Ordinations were performed with percent cover data from 90 species, with water depth, water temperature, dissolved oxygen (mg/l), conductivity, and pH included as covariates. Similar CCA ordinations were also performed with percent cover based on each species wetland category. Once ordinations were completed, correlations of the abiotic data with axis scores were also calculated. We further identified differences among treatments by performing a multi-response permutation procedure (MRPP) (McCune & Grace 2002), with Sørensen distance with field (North and South) and treatment (Soil-removed and Control) as the *a priori* groupings. Pairwise comparisons between treatments were tested to measure the strength of difference between the individual and combined treatments.

Results

Seed bank

The seed bank sampled prior to soil removal in 1999 contained 375 germinated plants from 24 species (App. 1). Soil closest to surface level (0-10 cm) had approximately three times more seeds germinate compared to the two deeper soil depth categories (Fig. 1a; $F_{2,42} = 32.81$, $P < 0.001$). The species richness of seedlings was also highest in the upper 0-10 cm soil depth (Fig. 1b; $F_{2,42} = 19.90$, $P < 0.001$). The ratio between annual (mostly arable weeds) and perennial species was about five times greater in the 0-10 cm soil depth compared to the two deeper soil depth categories (Fig. 1c; $F_{2,38} = 20.08$, $P < 0.001$).

Environmental conditions

Soils sampled in 2000 had lower percent organic matter ($F_{2,30} = 5.81$, $P < 0.01$) in the 0-20 cm and 21-40 cm soil depths (76% and 79% organic matter, respectively) than the 41-60 cm soil depth (85% organic matter). Organic content was higher ($F_{1,30} = 5.60$, $P < 0.024$) in the North field (83%) than the South field (78%).

The North field was marginally higher in elevation than the South field. As a result, soil-removed plots in the North field were only submerged after heavy rain events, but were saturated below the soil surface during the July 2004 sampling. In contrast, most of the soil-removed plots in the South field were submerged

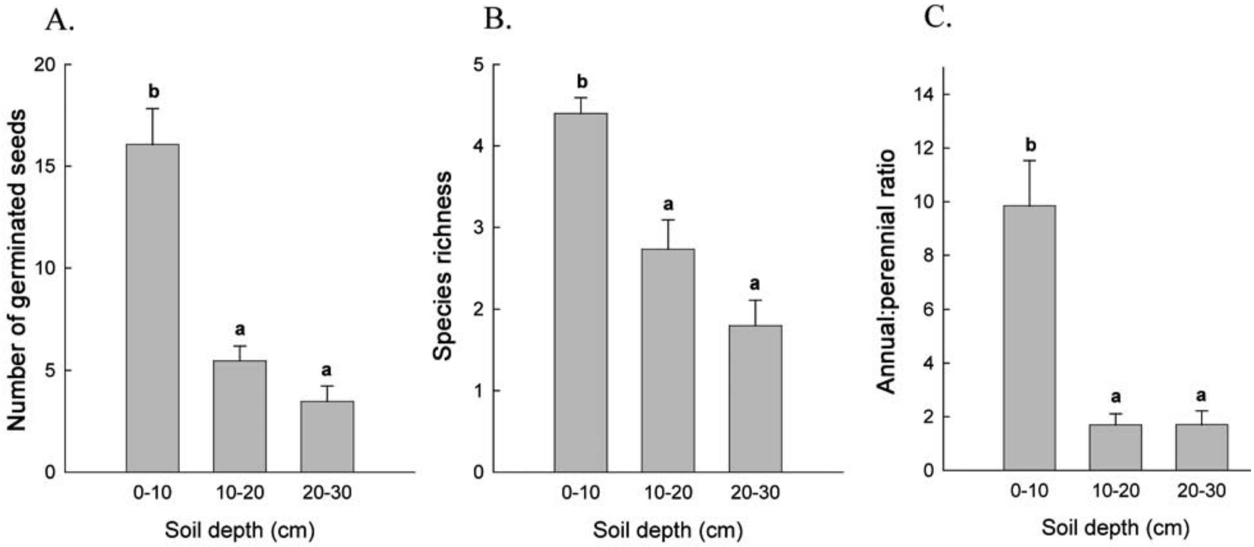

Fig. 1. Results from soil seed bank samples (10 cm^3) taken at three different depths (0-10 cm, 10-20 cm, 20-30 cm) showing: (**a**) number of germinated seeds; (**b**) species richness; and (**c**) annual:perennial plant ratio. Error bars represent ± 1 SE of the mean. Bars sharing the same letter are not significantly different using Tukey's LSD.

throughout 2004. Control plots in both fields were never flooded during sampling. The depth to the water table was significantly greater in the North field ($F_{1,20}$ = 6.84; P = 0.016) than the South field, and depth to water table was also lower in soil-removed plots ($F_{1,20}$ = 40.55, P < 0.001) compared to control plots. The soil-removed plots in the South field had ca. 13 cm of standing water while soil-removed plots in the North field had water ca. 9 cm below the soil surface. Water levels in control plots in the South and North field were 33 cm and 44 cm below the soil surface, respectively.

Water temperature was ca. 1 ºC higher in the South field than the North field ($F_{1,20}$ = 8.83, P = 0.007). Water in the soil-removed plots had slightly higher temperature ($F_{1,20}$ = 6.93, P = 0.002) and pH ($F_{1,20}$ = 4.19, P = 0.05), and much more dissolved oxygen ($F_{1,20}$ = 10.89, P = 0.0003) than control plots (Table 1).

Plant community responses

Above-ground biomass was higher in the North field (410.2g) than the South field (169.6 g) ($F_{1,20}$ = 16.24, P < 0.001) (Table 1), but no difference in biomass was detected between the soil-removed and control plots ($F_{1,20}$ = 0.01, P > 0.05). The Field × Treatment interaction was significant for species richness and Shannon-Weiner diversity ($F_{1,20}$ = 7.90, P = 0.01; and $F_{1,20}$ = 8.45, P = 0.008, respectively) (Table 1). The South field had significantly more species and higher diversity in the control plots, but the North field had significantly more species and higher diversity in the soil-removed plots (Table 1).

Table 1. Mean abiotic and biotic measurements and their respective P-values determined with 2-way ANOVAs. Field (North and South) and treatment – Control and Soil-Removed (S-R) – are factor variables, F × T = Field × Treatment interaction. P-values denoted as * are $P \leq 0.05$, ** are $P < 0.01$, and NS are $P > 0.05$.

	North		South		*P*-values		
	S-R	Control	S-R	Control	Field	Treat	F × T
Abiotic variables							
Water level (cm)	–9.07	–43.78	12.83	–32.72	*	**	NS
D.O. (mg/L)	1.410	0.683	1.416	0.758	NS	**	NS
pH	6.84	6.50	6.58	6.08	NS	*	NS
Temp. (ºC)	18.8	17.8	19.8	6.08	**	**	NS
Cond. (µS/cm)	444.7	785.7	496.9	18.6	NS	NS	NS
Biotic variables							
Biomass (g)	405.3	415.08	167.84	171.42	**	NS	NS
Species richness	23.83	15.33	13.00	20.00	NS	NS	**
Shannon diversity	0.94	0.64	0.61	0.78	NS	NS	**

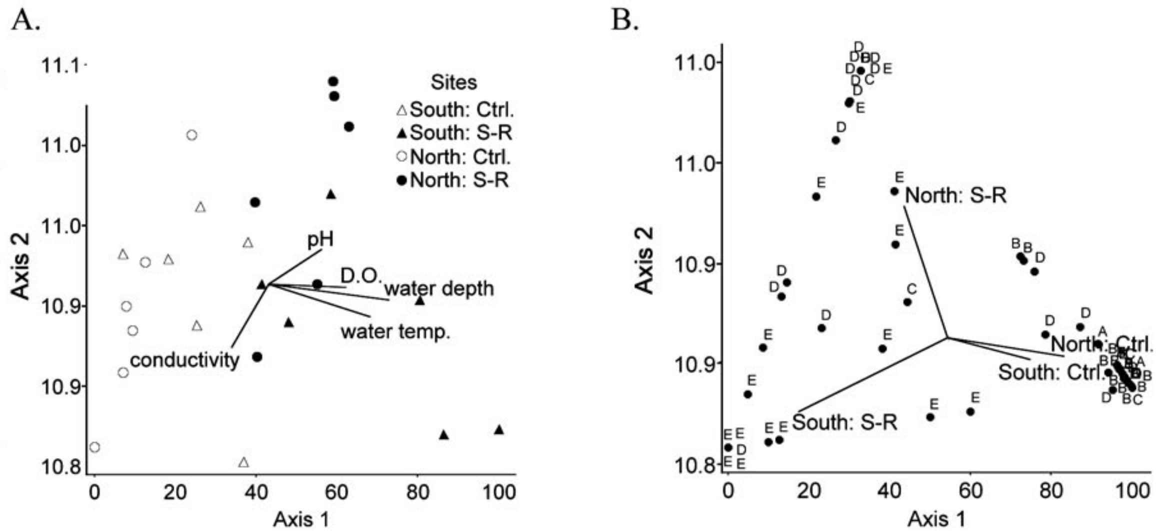

Fig. 2A. Ordination plots generated by Canonical Correspondence Analysis for patterns of plant percent cover for all 90 species. **B.** Depicts patterns of community separation based on percent cover for 69 species classified by Wetland Indicator values. (A = UPL, B = FACU, C = FAC, D = FACW, E = OBL) (S-R = Soil-Removed, Ctrl. = Control).

Canonical correspondence analyses (CCA) using percent cover of 90 species was run with water depth, water temperature, dissolved oxygen, pH, and conductivity as covariates. The first axis, accounting for 25.8% of the variance, separated the soil-removed plots from the control plots with abiotic variables of water depth (R^2 = 0.946), water temperature (R^2 = 0.637), and dissolved oxygen (R^2 = 0.356) strongly correlated in the direction of the soil-removed plots (Fig. 2A). In contrast, only conductivity (R^2 = 0.358) and pH (R^2 = 0.136) showed some correlation with Axis 2 however, 0% of the variance was explained by Axis 2. The MRPP identified clusters in the plant community associated with field location (North vs. South) and treatment (Soil Removed vs. Control) (P < 0.0001).

CCA was additionally run with percent cover for plant community types, identified by Wetland Indicator values, with a total of 69 species and 4 sites (2 Fields and 2 Treatment combinations) used as dummy variables (Fig. 2B). Axis 1 accounted for 45.9% of the variance and separated the soil-removed plots from the control plots. Even though the R^2 value for the North soil-removed plot for the second axis was 0.957, 0% of the variance is explained by Axis 2. No arable weeds were found in the soil-removed plots.

Discussion

Diamond (1975) coined the phrase 'assembly rules' to describe ecological rules that predict how communities are formed from the local pool of species that can potentially colonize a habitat. This concept has been applied to develop management strategies that determine the composition of animal and plant species that will be found in restored habitats (Keddy 1992, 2000). Our project was designed to identify how plant communities establish when natural wetland conditions are restored through soil removal and to classify the subsequent abiotic factors that exist. We found that community composition was strongly affected by soil removal but that small differences in elevation (in this case, ca. 15-20 cm) may affect the outcome of plant community assembly.

To understand the mechanics of plant community assembly rules, it is first necessary to identify the local species pool in the seed bank (Keddy 1992, 2000; Zobel et al. 1998). The results of our seed bank study supported the first hypothesis that the abundance, diversity, and annual:perennial ratio of germinated species would be greatest in the top 10-cm layer of soil. Consistent with Verhagen et al. (2001) and Bakker et al. (2005), we found that excavating 40-50 cm of surface soil removed most persistent agricultural weedy species in the seed bank, and as a result these species were restricted to control plots. Therefore, as a management objective, soil removal effectively reduced the pool of 'weedy' and invasive species (Verhagen et al. 2001; Bakker et al. 2005). However, changes in abiotic conditions (i.e. hydrology) had further impacts on the plant community.

Hydrology has been stated as the most important factor in the determination of wetland type and function, and restoring natural flooding regimes is a primary goal of wetland restoration (van der Valk et al. 1994; Hammer 1996; Keddy & Fraser 2000). Not surprisingly, our results showed that soil removal increased the water level (Dalrymple et al. 2003; Bakker et al. 2005). Other experiments have determined that an increase in water level, or flooding events, reduce the growth and affects morphological responses of wetland plants (Miller & Zedler 2003), especially seedlings (Barry et al. 2004; Kercher & Zedler 2004; Fraser & Karnezis 2005). Many arable weeds found in the seed bank study and emerged in control plots were not wetland plants (i.e. FAC and FACU species), and vulnerable to increases in water level. Therefore, the lack of arable weeds found in the soil-removed plots may be at least partially explained by increases in water level.

Agricultural soils often have elevated nitrogen levels (Wamia & Mackay 1996), which could increase the establishment and relative abundance of competitively superior invasive plants (Davis 2000) and lead to greater plant biomass. However, the second hypothesis that control plots would have a greater biomass than soil-removed plots was not supported by the data. This may mean that initial nutrient loads in the surface soil were low, or that the exposed peat in the soil-removed plots was sufficiently nutrient rich to support plant growth.

Our data supported the third hypothesis that plant community composition would be influenced by changes in the abiotic conditions between the control and soil-removed plots. Resulting plant community structure was dependant on field location and treatment type. Differences in hydrology explained the greatest proportion of variance for species distribution patterns even though other environmental variables (percent organic matter, water temperature, pH, and dissolved oxygen) were also significantly different between soil-removed plots and control plots. There seems to be a tolerance threshold that plants have to water levels, which corresponds with a recent study that assessed seedling survival and biomass accumulation for fourteen wetland plant species grown under different water depths from –6 cm to +6 cm relative to the soil surface (Fraser & Karnezis 2005). There is a wide range of tolerance limits to water depth between plant species. Similar patterns of plant community clustering were identified using CCA and MRPP when species were analysed for percent cover and wetland category status.

Due to the difference in elevation between the North and South field, approximately 80% of soil-removed plots in the South field were underwater or at water table while soil-removed plots in the North field had water levels ca. 9 cm below the soil surface. Therefore, this study also identified the effect of water depth on plant establishment in the soil-removal treatments. The North field had no standing water at the time the study was performed but may temporarily flood during high rain events. This potential hydrological heterogeneity supported significantly greater numbers of species and higher species diversity. The herbaceous community on the soil-removed plots in the North field was composed of many FACW or OBL wetland species (e.g. *Juncus effusus, Scirpus cyperinus, Carex lupulina,* and *Carex vulpinoidea*). In contrast, plants in soil-removed plots in the South field were mostly obligate (OBL) wetland plants (e.g. *Lemna minor, Typha latifolia, Ceratophyllum demersum,* and *Sparganium eurycarpum)*. These species are floating, emergent, or submerged life forms that were rare in the North field soil-removed plots.

Plant communities in the unmanipulated control plots served as the baseline of comparison and were distinctly different from communities in soil-removed plots. The North and South field control plots had similar water depth with no differences in species richness or species diversity detected between fields. Plant species that were typically found on the control plots included *Urtica dioica, Erigeron annuus, Polygonum persicaria, P. pensylvanicum* and *P. lapathifolium.*

This study demonstrates that using soil removal as a management tool had clear ecological benefits: it reduced invasive weeds and promoted obligate wetland plant species. Although our study was conducted at only one site in northeast Ohio, the restoration techniques followed standard operating procedures of the U.S. Army Corps of Engineers. It is important to note that the decision on how much soil to remove is important for ecological and economic reasons. Our results suggest that restoration managers should determine the distance to the ground water table and adjust the amount of soil removed to create the desired hydrology. For example, the soil-removed plots in the North field had an average water depth of approximately 10 cm below the soil surface, whereas the soil removed plots in the South field had a water depth of approximately 10 cm above the soil surface. The wet meadow community was more diverse in the North field and contained a greater number of desirable wetland plants. The same result could have potentially been accomplished in the South field if less soil was removed (ca. 20 cm; i.e. half of what was removed), which may have resulted in the same hydrology as the North field while still removing the weed seeds and significantly reducing the cost of excavation.

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References

Anon. 1990. *Memorandum of agreement between the Environmental Protection Agency and the Department of the Army concerning the determination of mitigation under the Clean Water Act Section 404(b)(1) Guidelines*. US EPA (Environmental Protection Agency and the Department of the Army), Washington, DC, US.

Anon. 1999. *JMPIN Version 3.2.6*. SAS Institute Inc. Cary, NC, US.

Andreas, B.K., Mack, J.J. & McCormac, J.S. 2004. *Floristic Quality Assessment Index (FQAI) for vascular plants and mosses for the State of Ohio*. Ohio Environmental Protection Agency, Division of Surface Water, Wetland Ecology Group, Columbus, OH, US.

Bakker, J.P., Esselink, P., Dijkema, K.S., van Duin, W.E. & de Jong, D.J. 2002. Restoration of salt marshes in the Netherlands. *Hydrobiologia* 478: 29-51.

Bakker, C., de Graaf, H.F., Ernst, W.H.O. & van Bodegom, P.M. 2005. Does the seed bank contribute to the restoration of species-rich vegetation in wet dune slacks? *Appl. Veg. Sci.* 8: 39-48.

Baldwin, A.H., Egnotovich, M.S. & Clarke, E. 2001. Hydrologic change and vegetation of tidal freshwater marshes: field, greenhouse, and seed-bank experiments. *Wetlands* 21: 519-532.

Barry, M.J., Bowers, R. & de Szalay, F.A. 2004. Effects of hydrology, herbivory, and sediment disturbance on plant recruitment in a Lake Erie coastal wetland. *Am. Midl. Nat.* 151: 217-232.

Blume, L.J., Schumacher, B.A., Schaffer, P.W., Cappo, K.A., Papp, M.L., Van Remortel, R.D., Coffey, D.S., Johnson, M.G. & Chaloud, D.J. 1990. *Handbook for methods in acid deposition studies laboratory analyses for soil chemistry*. EPA/600/4-90/023. Environmental Protection Agency, Washington DC, US.

Dahl, T.E. 1990. *Wetlands losses in the United States, 1780s to 1980s*. U.S. Department of Interior, Fish and Wildlife Services, Washington, DC, US.

Dahl, T.E. 2000. *Status and trends of wetlands in the conterminous United States, 1986-1997*. U.S. Department of Interior, Fish and Wildlife Services, Washington, DC, US.

Dalrymple, G.H., Doren, R.F., O'Hare, N.K., Norland, M.R. & Armentano, T.V. 2003. Plant colonization after complete and partial removal of disturbed soils for wetland restoration of former agricultural fields in Everglades National Park. *Wetlands* 23: 1015-1029.

Davis, K.J. 2000. *The effects of nitrogen manipulations and hydrology on the establishment and competitive abilities of wetland prairie plant species (western Oregon)*. Ph.D. Dissertation, Oregon State University, Corvallis, OR, US.

Diamond, J.M. 1975. Assembly of species communities. In: Cody, M.L. & Diamond, J.M. (eds.) *Ecology and evolution of communities*, pp. 342-444. Belknap Press, Harvard University Press, Cambridge, MA, US.

Fraser, L.H. & Karnezis, J.P. 2005. A comparative assessment of seedling survival and biomass accumulation for fourteen wetland plant species grown under minor water-depth differences. *Wetlands* 25: 520-530.

Fraser, L.H. & Keddy, P.A. 2005. *The world's largest wetlands: ecology and conservation*. Cambridge University Press, Cambridge, UK.

Gallihugh, J.L & Rogner, J.D. 1998. *Wetland mitigation and 404 permit compliance study, Vol.1*. U.S. Fish and Wildlife Service, Region III, Burlington, IL, and U.S. Environmental Protection Agency, Region V, Chicago, IL, US.

Hammer, D.A. 1996. *Creating freshwater wetlands*. 2nd. ed. CRC Press, Boca Raton, FL, US.

Hölzel, N. & Otte, A. 2004. Assessing soil seed bank persistence in flood-meadows: The search for reliable traits. *J. Veg. Sci.* 15: 93-100.

Jacquemart, A.L., Champluvier, D. & De Sloover, J. 2003. A test of moving and soil-removal restoration techniques in wet heaths of the High Ardenne, Belgium. *Wetlands* 23: 376-385.

Jungerius, P.D., Koehler, H., Kooijman, A.M., Mücher, H.J. & Graefe, U. 1995. Response of vegetation and soil ecosystem to mowing and sod removal in the coastal dunes 'Zwanenwater', the Netherlands. *J. Coastal Conserv*. 1: 3-16.

Keddy, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. *J. Veg. Sci.* 3: 157-164.

Keddy, P.A. 2000. *Wetland ecology: principles and conservation*. Cambridge University Press, Cambridge, UK.

Keddy, P. & Fraser, L.H. 2000. Four general principles for the management and conservation of wetlands in large lakes: the role of water levels, nutrients, competitive hierarchies and centrifugal organization. *Lakes and reservoirs: Research and management* 5: 177-185.

Kentula, M.E. 1996. Wetland restoration and creation. In: Fretwell, J.D. & Redman, P.J. (eds.) *National water summary on wetland resources*, pp. 87-92. U.S.G.S. Water Supply Paper 2425. U.S. Geological Survey, Washington, DC, US.

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

Leck, M.A., Parker, V.T. & Simpson, R.L. 1989. *Ecology of soil seed banks*. Academic Press, San Diego, CA, US.

Little, M. & Waldron, M.C. 1996. Ohio wetland resources. In: Anon. (United States Geological Survey): *National water supply on wetland resources,* pp 309-313. Water Supply Paper 2425. U.S. Government Printing Office, Washington, DC, US.

Marrs, R.H. 1993. Soil fertility and nature conservation in Europe: theoretical considerations and practical management solutions. *Adv. Ecol. Res.* 24: 2241-2301.

McCune, B. & Grace, J.B. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR.

McCune, B. & Medford, M.J. 1999. PC-ORD. *Multivariate analysis of ecological data*, Version 4. MjM Software Design, Gleneden Beach, OR, US.

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

Mitsch, W.J. & Gosselink, J.G. 2000. *Wetlands*. John Wiley & Sons, Inc., New York, NY, US.

Pfadenhauer, J. & Grootjans, A. 1999. Wetland restoration in central Europe: aims and methods. *Appl. Veg. Sci*. 2: 95-106.

Reed, P.B. 1988. *National list of plant species that occur in wetlands*. Department of the Interior, U.S. Fish and Wildlife Service, Washington, DC, US.

Tiner, R.W., Jr. 1984. *Wetlands of the United States: current status and recent trends*. U.S. Fish and Wildlife Service, National Wetlands Inventory, Washington, DC, US.

van den Berg, L.J.L., Vergeer, P. & Roelofs, J.G.M. 2003. Heathland restoration in The Netherlands: Effects of turf cutting depth on germination of *Arnica montana*. *Appl. Veg. Sci*. 6: 117-124.

van der Valk, A.G., Squires, L. & Welling, C.H. 1994. Assessing the impacts of an increase in water level on wetland vegetation. *Ecol. Appl*. 4: 525-534.

Verhagen R., Klooker, J., Bakker, J.P. & van Diggelen, R. 2001. Restoration success of low-production plant communities on former agricultural soils after top-soil removal. *Appl. Veg. Sci*. 4: 75-82.

Wamia, F. & Mackay, D. 1996: Tracking the distribution of persistent organic pollutants. *Environ. Sci. Tech*. 30: 390-396.

Zar, J.H. 1984. *Biostatistical analysis*. Prentice-Hall Inc, Englewood Cliffs, NJ, US.

Zedler, J.B. 1993. Canopy architecture of natural and planted cordgrass marshes-selecting habitat evaluation criteria. *Ecol. Appl*. 3: 123-138.

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

Zobel, M., van der Maarel, E. & Dupré, C. 1998. Species pool: the concept, its determination and significance for community restoration. *Appl. Veg. Sci*. 1: 55-66.

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