Spring 2013

Soil and Vegetation Changes across a Restoration Chronosequence: An Evaluation of Wetlands Reserve Program (WRP) sites in West-central New York, USA

Jordan Brown
The College at Brockport, jbrow7@brockport.edu

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Soil and Vegetation Changes across a Restoration Chronosequence:
An Evaluation of Wetlands Reserve Program (WRP) sites in West-central New York, USA

By

Jordan Brown

A thesis submitted to the Department of Environmental Science and Biology of The College at Brockport State University of New York in partial fulfillment of the requirements for the degree of Master of Science in Environmental Science and Biology

2013
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APPROVED BY:

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Advisor Date

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Reader Date

_______________________
Reader Date

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Chair, Graduate Committee Date
ACKNOWLEDGEMENTS

This work was completed with the help of several generous professors, practitioners, and students. I first and foremost acknowledge my major professor, Dr. Mark Norris. His contributions to this study and to my professional development are beyond measure. I will never be able to express how much I appreciated his knowledge, participation, and most importantly, patience. I also thank my remaining thesis advisory committee members, Dr. Douglas Wilcox and Dr. James Haynes. Dr. Wilcox gave me the confidence to work with and in wetlands and Dr. Haynes provided an encouraging tone along with several challenging, but constructive “big-picture” questions. This project would have been logistically unbearable without David Kitchie and Shanna Shaw of the Natural Resource Conservation Service. They helped me navigate through all the bureaucratic obstacles that would have otherwise made this study impossible. Along those same lines, I thank the landowners of my study sites, not only for granting me access to their private properties, but also for their hospitality and willingness to answer my questions thoughtfully. Lastly, I say thank you to several students in the Environmental Science & Biology Department, namely my labmate Justin Rogers, and undergraduates Cody Smeltzer, Chuck Froome, Nicholas Vermeulen, and Jeff Meyer, who provided a significant amount of hands-on assistance during field and laboratory work.
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1. ABSTRACT

Wetland restorations in the United States, including those sponsored by the federal Wetlands Reserve Program (WRP), are driven by the prospect of regaining critical ecosystem services lost during centuries of wetland destruction. Yet, service provision is contingent on the recovery of basic wetland functions, such as carbon (C) storage, which is especially tentative (and unverified) in WRP projects in west-central New York (WCNY), USA because those involve installing isolated wetlands on sites directly degraded by agricultural conversion. To assess recovery, I collected soil and vegetation data from 17 of WCNY’s WRP sites restored from tillage or non-tillage agriculture, aged 0-15 years since restoration at the time of sampling (August-October 2010). These were subjected to chronosequence-based analyses designed to detect divergence from a pre-restoration baseline (calculated using data from active agricultural fields paired to each WRP site) and/or convergence towards a “natural” condition (determined using data from four naturally-occurring, depressional, Palustrine Emergent wetlands within the same region). Restored WRP soils remained similar to agricultural soils in terms of organic matter, density, moisture, and belowground plant biomass across the chronosequences, indicating negligible C storage and soil development during the first 15 years. Additionally, soil development is limited in both post-tillage and post-non-tillage restorations and limited throughout the disparate habitat zone types that occur on these sites (upland meadows,
emergent-dominated shorelines, and permanent open-water areas). Plant metrics like vascular species richness, cover of certain qualitative groups, and biomass matched natural wetlands within 15 years. Yet, recovery of some metrics was only detected in previously tilled sites, while other metrics only displayed recovery in untilled sites. Additionally, recovery was often detected in only one of the three habitat zones, collectively suggesting that different plant metrics are differentially influenced by the conditions imposed by historical tillage and/or the zone in which they are measured. Vegetation analyses also showed that plant community recovery can be complicated when plant parameters in restoration sites “overshoot” beyond natural conditions. In conclusion, ecological recovery in WRP restorations in WCNY is variable, depending on metric, land-use history, and habitat zone. Although generally, many plant community features recover rapidly and despite limited recovery in soil physiochemical properties.
2. INTRODUCTION

2.1 FUNCTIONAL LOSSES FOLLOWING WETLAND CONVERSION

Wetlands have been described as crucial to the historical and future development of society, but their importance to humans stems from innate ecological functions (Mitsch and Gosselink 2007). The environmental conditions that distinguish wetlands from other ecosystem types give rise to wetland-specific functions and functional capacities. These functions are diverse and interlinked but can be grouped roughly into three main categories: habitat-related (e.g., breeding grounds for wildlife), hydrologic (e.g., groundwater recharge and discharge), or biogeochemical (e.g., nutrient cycling and storage) (Sather and Smith 1984, Smith et al. 1995). Wetland biogeochemical functions are complex and not fully understood (Adhikari et al. 2009) but are especially interesting because they have implications far beyond the wetlands in which they occur and often help define watershed- and landscape-scale features (Bedford and Preston 1988).

In addition to locally relevant biogeochemical functions, wetlands are globally important belowground carbon (C) storage sites (Euliss et al. 2006). Wetland soils can capture and retain vast quantities of C and, thus, can be substantial sinks of atmospheric C (Mitra et al. 2005). It has been proposed that, collectively, these natural C sequestration processes have the potential to substantially draw down atmospheric C levels to the point of partially

Despite the varying ecosystem services of wetlands, from species refugia to climate stabilization, wetlands have incurred major losses in the United States (U.S.) (Dugan 1993). Dahl (1990) estimated that wetland area in the U.S. was reduced by over 50% between 1780 and 1980. This trend of habitat destruction coincided with a large, anthropogenic shift in land-cover driven mostly by the process of agricultural conversion (Zedler and Kercher 2005) whereby naturally occurring wetlands were physically altered to support farmland (Frayer et al. 1983, Vileisis 1997, Osteen et al. 2012).

Conversion of any ecosystem to an agrosystem often involves significant alterations to ecosystem structure and function. To grow crops, improve grazing for domestic animals, and facilitate the use heavy farm machinery, farmers remove native vegetation, disturb soils and, in the case of converted wetlands, alter hydrology (Lilly 1981). Nearly all ecosystem attributes can be changed by intensive agriculture (Matson et al. 1997), but in light of global climate change, some of the most important changes to wetlands involve belowground C dynamics.

2.2 TILLAGE AGRICULTURE DEPLETES SOIL ORGANIC CARBON
In soil, C is contained within organic and inorganic complexes. Inorganic soil C is a substantial part of the global C budget and important in the global C cycle (Wu et al. 2009), but soil organic carbon (SOC) is many times more abundant and critical to several soil functions such as aggregate formation, soil temperature moderation, chemical buffering, and plant nutrient retention and, therefore, corresponds with many aspects of “soil quality” (Lal 2004). It is often considered as a fraction of soil organic matter (SOM), which more generally refers to all organic matter (OM) in soil and extends to include the non-C constituents of plant and animal residues, living soil microbes, and humic substances.

However it is considered, SOC is sensitive to land-cover/land-use changes. Conventional tillage, in particular, causes rapid changes in SOC levels by offsetting the natural balance between organic C outputs and inputs (Post and Mann 1990). The magnitude and direction of soil C change following cultivation depends on many variables, including the duration and intensity of soil disturbance and pre-cultivation C levels (Mann 1986), but the net result is commonly C loss (Davidson and Ackerman 1993) likely through decreasing C inputs to soil and/or increasing C outputs (through enhanced decay).

Soil organic C is mostly plant-derived (Kögel-Knabner 2002), so its formation primarily begins with photosynthesis, which fixes atmospheric
carbon dioxide (CO₂) into solid, organic C during the formation of biomass (stems, leaves, roots, fruits, etc.), otherwise known as net primary production (NPP; kg C m⁻² year⁻¹). Any biomass or OM that remains on site as detritus may become SOM if incorporated into the soil profile. Yet, removing plant biomass (i.e., harvesting crops) limits detritus accumulation and, thus, the potential for SOM accumulation. Also, if harvested biomass includes photosynthetic tissues, it can decrease the overall influx of C from the atmosphere by arresting the fixation process.

Mass balance equations for SOC (e.g., Lal 2003) state that continued depletion of C pools in agricultural soils may not only be a consequence of decreasing C inputs, but also of increasing C outputs. The processes that underlie outputting are biochemical or physical and, while natural, are easily enhanced by tillage. Biochemical soil C loss occurs as soil heterotrophs (primarily microbes) decompose and metabolize SOM complexes as energy sources and, during respiration, convert solid SOC to an oxidized form (gaseous CO₂) which is readily lost to the atmosphere.

Oxidation of SOC is ultimately regulated by how chemically resistant the SOC complexes are to microbial attack, but actual oxidation rates also depend on the degree of protection afforded to SOC complexes by the mineral matrices in which they exist (Baldock and Skjemstad 2000). As soil aggregates form, they can encapsulate SOM and make it inaccessible to
microbes (see Krull et al. 2003 for a comprehensive discussion of SOC/SOM stabilization). This form of structural protection may break down following agricultural conversion because soil agitation (i.e., tillage) ruptures aggregates and exposes the previously protected SOC within to microbes (Craswell and Waring 1972, Street 1982, Jiao et al. 2006).

Undisturbed wetlands also provide environmental protection to SOC complexes. Whether environmental conditions favor SOC accumulation is largely a function of state factors such as climate (McLauchlan et al. 2006, Bernal and Mitsch 2008), which do not change during land-use conversions, but also depends on more local factors (NPP, soil composition, hydrology), all of which can be immediately impacted and even regulated by agriculture. Altering hydrology for agricultural purposes (e.g., interrupting natural patterns of inundation via draining) is particularly important. Draining (and plowing) removes the inhibitory effect of soil anoxia on aerobic microbial activity and allows respiration to outpace SOM stabilization (Portnoy 1999, Sahrawat 2004). Collectively, oxidative reactions seem to drive most C loss, at least during the initial years of cultivation (Gregorich and Anderson 1985).

Physical carbon loss through erosion is also likely. This process is a common side-effect of tillage agriculture and is the primary cause of soil degradation worldwide (Pimentel et al. 1995, Scherr 1999). It involves the detachment, breakdown, transport, and deposition of soil particles from one
site to another via wind or flowing water. The off-site transport of soil (and the C therein) not only decreases on-site soil quality directly and indirectly perpetuates soil degradation by hindering future plant productivity (Gregorich et al. 1998), it also promotes C loss by oxidation. That is, oxidative and erosional losses are often coupled because the breakdown actions of erosion can rupture soil aggregates in ways similar to tillage and lead to gaseous C losses during transport and deposition (Lal 2003). In general, conventional tillage agriculture necessitates major disturbances to soils that, along with the removal of vegetative covers, push soil systems toward C loss and away from C accumulation and storage (Corsi et al. 2012).

2.3 RESTORATION TO COUNTERACT WETLAND LOSS

The historical trend of agricultural conversion was reinforced and exacerbated by a common perception that ag land was more valuable than the native ecosystems they replaced (Heimlich et al. 1998). As such, tillage agriculture has become and remains integral to global food production. Yet, as our understanding of its effects on soil C storage and other ecosystem functions has increased, so has our interest in mitigating these effects. The functional capacities of wetlands and the functional shortcomings of many agrosystems became a policy issue only after ecosystem functions were translated to ecosystem services - the outcomes of naturally occurring functions that are directly or indirectly beneficial to humans (Dahl and Allord
That is, the widespread recognition of functional wetlands as a “public good,” initiated the relatively recent phenomenon of active wetland protection (Dahl 2000, Mitch and Gosselink 2007).

In the 1970s, the U.S. passed several pro-wetland laws that culminated with the adoption of “no net loss,” a federal wetland management policy stipulating that the nation must maintain the amount wetland area in the country (Heimlich et al. 1998). Implementation of this policy is not specified by a single piece of legislation. Instead, the U.S. relies on numerous governmental agencies to enforce and manage an even greater number of laws and programs that discourage or counteract wetland destruction. These, along with non-governmental efforts, collectively help conserve the national wetland resource base through preservation, mitigation, and restoration.

Given the amount of wetland area that has already been degraded, restoration has enormous potential as a wetland conservation strategy. A noteworthy example of a wetland restoration program is the Wetlands Reserve Program (WRP). The WRP is one of many conservation initiatives directed by the U.S. Department of Agriculture (USDA) that uses financial incentives to encourage U.S. farmers and ranchers to address environmental issues on their lands voluntarily (USDA-NRCS 2009). Its progenitor, the Conservation Reserve Program (CRP) is broadly oriented towards the protection and enhancement of soil and water resources in areas affected by
commercial agriculture. Yet, the WRP, like the Grasslands Reserve Program (GRP) and the Healthy Forests Reserve Program (HFRP), deals with a specific ecosystem type.

The WRP was established by the Food, Agriculture, Conservation and Trade Act of 1990 (the 1990 Farm Bill) and was reauthorized by the Food, Conservation, and Energy Act of 2008. It is administered by the USDA’s Natural Resource Conservation Service (NRCS). The NRCS secures financial and technical assistance for landowners who have chosen one of three enrollment options: permanent conservation easement, 30-year conservation easements, or a non-easement restoration cost-share agreement. Each contract allows landowners to retain legal ownership of the land, but they must adhere to WRP conservation goals on all enrolled area. This means, primarily, that the landowners surrender the right to alter the restoration site substantially, but they retain the right to control access and to take part in limited recreational activities like hunting and trapping. Most WRP projects involve the restoration of wetlands that have been essentially destroyed by draining, dredging, filling, and cropping or otherwise degraded by pollution, grazing by domestic animals, or other agricultural stresses. These restorations usually take place on portions of private land that have been voluntarily idled or are of marginal value as crop fields or pasture.
As restorations, WRP projects aim to reverse the impacts of agriculture (see Section 2.2) and restore wetland functions and values. While the C storage functions of soil may resume naturally following the cessation of agriculture (Guo and Gifford 2002), active restoration of degraded systems is thought to accelerate recovery (Dobson et al. 1997, Baer et al. 2002, Meyer et al. 2008) and help guide community development along more desirable successional trajectories (Mitsch and Wilson 1996, Kardol et al. 2005). Thus, restorations are investments toward speedier ecosystem-level recoveries and more precise ecological outcomes (Dobson et al. 1997). Still, ecosystem responses to any restorative measure can be difficult to predict, and there is some uncertainty regarding the efficacy of many restorations (Suding et al. 2004). To address these uncertainties and to advance the science of ecological restoration, a fair amount of research has been dedicated to evaluating completed wetland restorations.

2.4 EVALUATING ECOSYSTEM RECOVERY WITH SOIL CARBON

If and how evaluations are conducted is dictated by project goals, compliance standards, and analytical resources, but many restoration projects include ~5 year monitoring phases that follow compositional or structural changes (e.g., plant community dynamics) that occur after implementation (Mitsch and Wilson 1996). In addition to being deficiently short-term (D'Avanzo 1990, National Research Council 2001), such
measurements are mostly useful for *community-level* evaluations and much less informative about the functional development of ecosystems (Kelly and Harwell 1990).

Ecosystem-level evaluations require the use of functional indicators that reveal if and how ecosystem functions are occurring. All functions imply interactions between the biotic and geochemical constituents of a system and, therefore, could be telling of the individual components. However, the function of C storage is interesting in and of itself because (1) it is closely linked with other important wetland processes such as plant growth, nitrogen cycling, and faunal population support (Davidsson and Stahl 2000, Craft and Sacco 2003, Burchell et al. 2007), (2) holds some potential to mitigate climate change (see Section 2.1), and (3) it is an archetypal wetland function and a common restoration goal.

Carbon accumulation rates are readily calculated with soil C data but are often inferred using SOM data. Soil organic matter is a popular proxy measurement because it is highly correlated with soil C by weight (any amount of SOM is roughly 50% SOC; Pribyl 2010). It is also statistically correlated with important soil processes such as respiration (Howard and Howard 1993) and denitrification (Brettar and Höfle 2002), and, in general, is a useful indicator of soil development (Bruland and Richardson 2006, Meyer et al. 2008). To date, it is common for restored wetlands (Bruland and
Richardson 2006, Gleason et al. 2008) and wetlands constructed for mitigation purposes (Stolt et al. 2000, Campbell et al. 2002, Fennessy et al. 2008) to contain less SOM than their natural counterparts. However, snapshot comparisons of natural and restored wetlands may be misleading due to differences in ecosystem age and functional time-lags. Hence, simply determining if and at what rate restored wetland soils are approaching the condition of natural wetlands is a more laudable research goal.

Calculating SOM accumulation rates requires multiple data points spanning several years. Continuous long-term data for individual sites are rare; so many studies of post-restoration soil development rely on chronosequences. Meyer et al. (2008) studied a series of six restored palustrine wetlands in Nebraska, USA ranging in age from one to seven years since restoration, and Ballantine and Schneider (2009) analyzed a group of 35 depressional wetlands in New York ranging in age from 3-55 years. Both studies found SOM in the uppermost soil horizons to increase as a function of time and went on to conclude that, if SOM accumulation remained linear, SOM in those restored wetlands would reach “natural” levels in 20-30 years. On the other hand, Hossler and Bouchard (2010) calculated much slower accumulation rates for SOC from a series of freshwater marshes in Ohio and suggested a recovery time of approximately 300 years. Although vastly different, these recovery estimates may be accurate for their respective...
wetlands and the variation may simply reflect intrinsic differences among the wetlands under study (soil properties, restoration treatments, etc.).

If the condition of the restoration sites cannot explain the large variation in accumulation rates, the calculations may have been skewed by the chronosequences themselves. Chronosequences are essentially “space-for-time substitutions” that replace temporally-explicit sample points with spatially-explicit sample points that differ with respect to some temporal characteristic (e.g., ecosystem age; Pickett 1989). The goal is to isolate the effect of age on other aspects of the study system (e.g., ecosystem structure and function). Of course, in a field study, controlling for all variables besides site age is not feasible and researchers can only hope to minimize error associated with intrinsic site differences other than age. For example, Ballantine and Schneider (2009) restricted their study wetlands to those restored under a particular restoration program, thus, largely controlled for restoration methodology. Failing to account for variables such as restoration methodology may obscure significant relations between time and soil C.

This issue was highlighted by Gleason et al. (2008), who found that SOC did not consistently increase with restoration age and suggested that age-related patterns were indistinct, in part, because the chronosequence included sites with different land-use histories. At the time of restoration, some sites had accrued less agricultural disturbance and, as a result, had
more SOC to begin with and less potential to act as C sinks. This suggests that (1) sites with different pre-restoration conditions (land-use history) may respond differently to restoration efforts and (2) variables like land-use history may invalidate chronosequences if not properly factored into the analyses.

2.5 STUDY OBJECTIVES AND HYPOTHESES

Here, I addressed some important knowledge gaps regarding ecosystem recovery in WRP wetland restoration sites in west-central New York. In this region, the WRP has been consistently active since circa 1992 (NRCS staff, personal communication), but prior to this study, SOC/SOM accumulation in these sites has never been evaluated. Without confirmation from these data, these federally-funded restorations cannot do much to serve the national conservation policy of “no net loss.” That is, these sites cannot be accepted as full functional compensations for historical and contemporary wetland destruction nor can they be assumed to perform C-related ecosystem services (e.g., climate change mitigation through C sequestration).

With WRP sites ranging in age from 0 to 15 years since restoration, I used multiple, chronosequence-based approaches to evaluate several aspects of ecosystem recovery following the cessation of agriculture and the implementation of active restoration techniques. Evaluation methods were focused on SOM because of its relevance in soil development and ecosystem service provision, but extended to other soil properties and select vegetational
metrics. Analyses included (1) simple comparisons of differently aged WRP easements and of WRP easements against reference sites and (2) more refined chronosequence analyses that continuously tracked changes while controlling for potentially confounding factors such as land-use history. The simple comparisons aimed to show how SOM (and other measurements) varied among the study sites (which included WRP sites of different age classes, natural wetlands, and active agricultural fields) as in:

**H₁:** If sites are grouped into general land-use history categories, SOM would be lowest in active ag fields, low in the youngest restorations, high in the middle-age restorations, higher in the oldest restorations, and highest in natural wetlands. That is, SOM in the five land-use categories would rank according to presumed disturbance regimes (if and how recently the sites were disturbed by the agricultural activities that deplete SOM).

Restorations in the study not only varied by age, but also with respect to land-use history (tilled or untilled prior to restoration). As such, I performed chronosequences analyses designed to determine simultaneously if SOM, etc. changed consistently with wetland age (as opposed to age class) and in what direction:

**H₂:** In WRP sites specifically, SOM will increase linearly with wetland age (years restored) as the discontinuation of agricultural disturbances and intrinsic wetland attributes allow continuous SOM accumulation.
Hypothesis 2 served as the hypothetical foundation on which to test the influence of land-use history on age-related trends:

**H$_3$:** Any linear, age-related changes in SOM in WRP sites will vary by prior land-use; SOM will increase at a higher rate in historically tilled sites (with highly disturbed soils and high C sink potential) than in sites previously used as untilled pastures and/or no-till hayfields (with limited soil disturbances).

Sampling in each wetland was also stratified by specific habitat or plant community type. These habitats types (hereafter referred to as “zones”) were common to all sites and occurred based on hydrotopographic variables (e.g., elevation relative to water table, water depth, soil moisture). The biological and physical disparities among the zones were suspected to give rise to zone-specific patterns of productivity and decomposition, so I hypothesized that:

**H$_4$:** Linear SOM increases will be lowest (or least detectable) in areas of open water with submersed aquatic vegetation or no vegetation, intermediate in more upland meadow habitats, and highest in lowland areas dominated by emergent vegetation (which I suspected to have the highest ratio of NPP to aerobic decomposition).
3. METHODS

3.1 STUDY SITES

Field sites were restricted to private properties in west-central New York, USA (Fig. 1; precise site locations are withheld to comply with landowner privacy agreements). Wetland restoration sites included 17 active WRP contracts that were, prior to restoration, either tilled for crop production \((n = 12)\) or used for agricultural purposes not involving tillage such as pasture or no-till hayfield \((n = 5)\). Tilled sites had been restored for \(0 (n = 1), 2 (n = 1), 3 (n = 2), 5 (n = 1), 7 (n = 1), 10 (n = 2), 11 (n = 1), \) and \(12 (n = 2)\) years at the time of sampling. Untilled restorations had been restored for \(0, 1, 6, 10, 15\) years and included one site per age. General agricultural histories were ascertained through discussions with the landowners and by referencing historical imagery and farm records when available. According to the Web Soil Survey (USDA-NRCS 2011b), underlying soil textures at these sites were most commonly silty loams but ranged from silty clay loams to mucky silt loams.

For reference sites, I sampled four naturally occurring wetlands that had not incurred major mechanical disturbances in the last 50 years. These reference sites were geomorphically depressional (Brinson 1993), Palustrine Emergent wetlands (Cowardin et al. 1979) whose zones of persistent emergent vegetation were immediately surrounded by seasonally flooded
forest \((n = 3)\) or sparsely wooded meadow \((n = 1)\). Like WRP wetlands, these natural wetlands occurred as discrete habitat patches within predominantly agricultural landscapes and often shared abrupt borders with active ag fields, rural roadways, and residential land. Exact ages of these reference sites were unknown, but their developments preceded these restored wetlands by several centuries or millennia and were assumed to have reached near steady-state C balances.

For additional references, each WRP and natural wetland was paired with an active agricultural field (hereafter “ag field”). Ag fields were geographically (within 100 m) and topographically near their corresponding wetlands and, in the case of the WRP sites, assumed to approximate the pre-restoration condition of the nearby restoration site (as confirmed by the landowner). That is, each formerly tilled restoration site was paired with a currently tilled field, and each formerly untilled restoration site was paired with an untilled field that was currently being used for pasture or no-till cropland. These fields were sampled to determine the differences among different land use types \(i.e.,\) agricultural land vs. restored wetland vs. natural wetland) and to calculate post-restoration changes (see Section 3.10.1).

3.2 SAMPLING POSITIONS

The number of inundated basins within easement boundaries varied among restoration sites (from 1 to 16), along with the basin shapes (circular
to polygonal), and basin sizes (0.03 to 3.5 hectares). Some basins included small islands, and in some sites with multiple basins, basins featured temporary or permanent surface-water connections in the form of spillways or ditches. However, all sites included the same general zones. For this study, I considered three: the (1) meadow zone, (2) emergent zone, and (3) open-water zone.

The open-water zones comprised the permanently inundated portions of each basin and corresponded with Aquatic Bed habitats described by Cowardin et al. (1979), as they contained either floating and submersed aquatic vegetation or no vegetation. The emergent zones encompassed the emergent plants that occurred near the basin shorelines and qualified as Persistent and Non-persistent Emergent Vegetation habitat (Cowardin et al. 1979). Plant assemblages in these zones were dominated by facultative or obligate wetland species. The meadow zones included the mostly upland habitat that surrounded the emergent vegetation. Meadow zones were always found at higher elevations relative to the emergent and open water zones and commonly developed atop the dikes/embankments that contained the basins. These areas featured both facultative and upland plant species. At all sites, these zones were delineated visually, as they were geomorphically and/or vegetatively discrete at the $1 \text{ m}^2$ resolution required by this study.
At each WRP wetland, three transects were established perpendicular to the basin's shoreline (Fig. 2). To capture any inter-basin variability in sites with multiple basins, I randomly selected 2-3 basins from those available, then laid 1-2 transects in each of them. Transect locations were determined by first selecting three randomly generated compass bearings. Then, deeming the approximate center of the open water zone as an origin, I used a compass to lay a transect in line with each bearing. Each transect was divided into three sections, each spanning a zone. I recorded the length of each transect section and, hence, the width of its corresponding zone. I used this flexible method of transect establishment over fixed-length transects to (1) ensure that I sampled the functionally-distinct zones throughout the restoration areas and (2) to analyze site attributes at a finer resolution than would be possible if sites were treated as homogenous habitat patches (see Section 2.5, H₄).

I laid a 1 m² quadrat along and at the approximate midpoint of each transect section so that there were three sampling plots per zone and a total of nine per site. Although there were sharp transitions between the wetland zones I delineated, quadrats were laid purposely on transect section midpoints to ensure the samples purely represented the wetland zone and not the narrow transition zones.
Transects and plots were established similarly in natural wetlands, but these sites had different patterns of zonation; they lacked distinct open-water zones. Also, the areas immediately peripheral to the emergent marsh were either dominated or sparsely occupied by mature, bottomland hardwoods (*e.g.*, *Fraxinus pennsylvanica* Marsh.). So, I considered only two wetland zones in the natural wetlands: the emergent zone and the peripheral zone. During analysis, the emergent zone of the reference sites corresponded to the emergent zones of the WRP wetlands, while the peripheral zones corresponded to the WRP meadow zones. Without open-water zones, the reference sites had a total of six sampling plots.

3.3 FIELD INVENTORY AND SAMPLE COLLECTION

Visual estimations of percent cover for living vascular plants (by species, non-vascular plants by genus or division, bare ground, and standing water took place within each 1 m\(^2\) quadrat between mid-August and early-September 2010. Nomenclature primarily followed USDA-NRCS PLANTS Database (2012) but was cross-referenced and supplemented with the Integrated Taxonomic Information System on-line database (2012).

Aboveground, herbaceous plant biomass (live and dead) was harvested from the center of each plot within a 0.1225 m\(^2\) subplot immediately following cover estimates. Cover estimations excluded woody plants ≥ 1 m in height, and biomass harvests excluded tree leaves occurring ≥ 1 m above the ground.
and woody tissues. This was meant primarily to exclude the sampling of mature trees in the natural wetland sites, as only 3% of WRP sampling quadrats contained large woody plants.

Between early- and mid-October 2010, from the center of the subplots, I measured water depth (cm) and removed one soil core (20-cm depth, 5-cm diameter) by driving a polyvinyl chloride (PVC) tube into the substrate. Removing cores from underwater was done with a longer section of the same tubing. In those instances, I rested the tube atop the consolidated surface sediments in the center of the sub-quadrat, allowed it to backfill with water, drove it down 20 cm, sealed the top with an air-tight cap, and then slowly removed the core. The suction created by sealing the top of pipe prevented the soil core from washing out under the weight of the backfilled water upon removal. After removing the cap, water in the pipe was slowly poured off until only a solid core remained.

Three additional cores were taken from each active ag field that was paired with a wetland site. In these fields, soil extraction points were randomized by imagining the fields as regularly shaped grids and coring at three random coordinates relative to the corner of the field nearest the wetland (with coordinates 0 m, 0 m). However, I only used extraction points that fell on topographic positions similar to those of the adjacent wetlands to maximize comparability. All cores were placed in sealable plastic bags.
immediately after extraction and temporarily stored on ice before being transferred to longer-term storage at 4°C along with the plant biomass samples.

3.4 SOIL ANALYSES

I weighed and calculated the volume (cm\(^{-3}\)) of the field-moist soil cores immediately following removal from cold storage. I removed macro-invertebrates, roots, and rhizomes by hand while passing the cores through 4-mm sieves. Cores were not separated into depth fractions primarily to minimize sample processing time, but also because study sites had highly disturbed soils that lacked distinct horizons. From each sieved and homogenized soil sample, I analyzed a 30-40 g subsample for soil gravimetric moisture (%) by determining evaporative weight loss after drying at 105°C until constant mass. From each soil moisture reading, I calculated a moisture correction factor (subsample wet weight ÷ subsample dry weight) for each soil core and applied that to the corresponding core’s wet weight. This yielded corrected dry weights for the intact cores, which, along with the soil core’s volume, was used to determine bulk density (g cm\(^{-3}\)) for each core.

Two 8-10 g portions of soil were taken from each subsample previously dried for soil moisture analysis and analyzed further for SOM content via Loss On Ignition (LOI). These sub-subsamples were placed in loosely lidded ceramic crucibles, then dry combusted in a box furnace.
(BF51800 Series, Lindberg/Blue M, USA) for 3.5 hours at 400°C. Weight loss after combustion was calculated to determine ash free dry mass of the SOM (g). Dry mass values were used to calculate percent SOM (ash dry mass of SOM + pre-combustion dry mass of soil portion × 100). After confirming that percent SOM values were similar between duplicate portions (≤ 1% error), they were averaged to yield one value for each soil core. The percent SOM and bulk density value of each core were used to calculate SOM content (g m\(^{-2}\)) for the top 20 cm of soil of the plot from which the core was removed.

Equal portions of field-moist, sieved soil from triplicate cores (summing to approximately 450 cm\(^3\)) were combined in PVC cylinders (10-cm diameter, 7.5-cm height). The bottoms of these cylinders were covered with a fine mesh, and the tops were covered with plastic wrap permeable to CO\(_2\) but not to water vapor to slow soil desiccation without causing accumulation of CO\(_2\). The mesh and plastic wrap sections were secured to the cylinders with rubber bands. To take measurements of C efflux (g m\(^{-2}\) day\(^{-1}\)) from these microcosms, I placed them on a level surface, brought their soils to field/container capacity by slowly adding water until water flowed out the bottoms, and aerobically incubated them at 25°C for 29 days. Twenty-four hours after water additions, I began analyzing the headspace gas every 6-7 days for CO\(_2\) using a LI-6400 Soil CO\(_2\) Flux System (LI-COR Biosciences, Lincoln, Nebraska).
Efflux rates from these composite soil samples were plotted over time as line graphs, and the area under the line was trapezoidally estimated using the “Area below curves” macro in SigmaPlot 11.0 (Systat Software, Inc., San Jose California, USA). These area values were the cumulative amounts of C respired from each microcosm over the duration of the incubation and were expressed as quantities of soil potentially mineralizable carbon or soil PMC (g m\(^{-2}\) of topsoil). While these values did not indicate actual decomposition rates or the amount of C that is respiring from the field sites, they did indicate the size of each zone’s labile C pool and, thus, showed which zones were most vulnerable to soil C loss via microbial respiration.

3.5 PLANT COMMUNITY AND BIOMASS MEASUREMENTS

Observed taxa were classified based on life-form (bryophytes, ferns, forbs, graminoids, shrubs and tree seedlings, and submersed/ floating aquatics), Northeast Region wetland indicator status (WIS) following USDA-NRCS PLANTS Database (2012), and Chadde (2002) (see Table 1 for WIS interpretations). Species were also classified as “invasive” if they were officially documented as being targeted by government plant control measures in New York or surrounding states (various sources). Plant community metrics included relative cover by life-form, WIS, and invasiveness, richness (average number of vascular plant species per m\(^{-2}\)), and the Shannon Index (H’) of biodiversity, modified so that “zero” values
indicated no species present and “one” values indicated one species present. This was done to mathematically accommodate the quadrats with no plant cover, which were relatively common in open-water zones and newly restored sites. All measurements from triplicate plots were averaged to yield a single mean value for each zone of each wetland.

Each aboveground plant biomass sample was sorted into current year’s biomass (living aboveground biomass; LAB) and biomass produced during previous years (litter mass) using color and textural indicators. Separated samples were oven-dried at 60°C until constant mass. Litter mass and LAB dry weights from each sub-quadrat were combined to produce total aboveground biomass (TAB) values (g m\(^{-2}\)). Litter mass and LAB were not calculated for plots in the open-water zones (only TAB values), as these samples contained plant tissues that could not be sorted precisely.

Fine root (root diameters < 2 mm), coarse root (root diameters ≥ 2 mm), and rhizome fragments were removed from each soil core, rinsed, dried at 65°C until constant mass, and weighed separately. Fine and coarse root weights were combined with rhizome biomass to calculate total belowground plant biomass (TBPB). Weights were converted to g per m\(^2\) of topsoil by multiplying the biomass by a volumetric correction factor [soil core volume ÷ (1 × 1 × 0.2 m volume of soil)].
3.6 STATISTICAL ANALYSES

3.6.1 Response Variables

Response variables were classified as aboveground variables (water depth, aboveground plant biomass, plant compositional metrics), belowground variables (SOM, soil PMC, soil bulk density, soil moisture, belowground plant biomass), or belowground changes. For belowground changes, I estimated post-restoration belowground changes by calculating the proportional difference between wetlands and their corresponding ag fields. These differences were computed under the assumption that each ag field approximated the pre-restoration condition of its corresponding wetland and are reported as percent changes: \( [(X_{\text{wetland}} - X_{\text{ag field}}) ÷ X_{\text{ag field}}] \times 100 \). For ease of comparison, this formula was also used to quantify the differences between natural wetlands and their corresponding ag fields, though those wetlands have no pre-restoration condition. It should also be noted that, when SOM is expressed as a percent, percent change is reported as absolute percent change and not as a relative percentage. Aboveground changes were not calculated because aboveground variables were not measured in the ag fields.
3.6.2 General Land-use History Comparisons

I first hypothesized that plant community characteristics and soil properties would vary among sites with different land-use histories because those histories imply different degrees of environmental disturbance (see Section 2.5). To address this, I sorted all sites into five, broad categories depending on their general land-use histories (which included an age component). Restored wetlands were split into Young Restorations (restored for 0-3 years), Middle-age Restorations (restored for 4-10 years), and Old Restorations (restored for 11-15 years), while all Natural Wetlands comprised their own group. Tilled and untilled ag fields were grouped together as Active Ag Fields because they were found to be statistically similar with respect to nearly all study variables (results not shown).

Although measurements were taken from three disparate zones in each wetland (see Section 3.2), General Land-Use History Comparisons only considered one observation per wetland (the average of the observations from each zone). These site-level averages were weighted based on the estimated area of each zone to correct for the fact that all restoration areas and natural wetlands used in this study had different and unequal proportions of meadow, emergent, and open-water habitat. Site-level averages for Active Ag Fields were straight means, as these sites were homogenous patches of either tilled or untilled ag field. Calculating and comparing these average
values allowed for the discussion of WRP restorations at the scale of whole sites (all area, wetland or otherwise, within the official easement boundaries), which more closely matches the scale at which these sites are considered legally.

Differences among categories with respect to response variables were examined using One-way Analysis of Variance (ANOVA) at $\alpha = 0.05$. Levene’s Test was used to detect heteroscedasticity and to select the appropriate multiple comparisons post-hoc test (Tukey’s when variances were homogenous and Games-Howell when equal variances were not assumed). Non-normal datasets were log-transformed as needed. When normality could not be assumed nor achieved via data transformation, I used Kruskal-Wallis One-way ANOVA on Ranks to compare the median values of each land-use category followed by the Dunn’s Method for multiple comparisons. Only four land-use history categories were compared with respect to aboveground variables because these were not measured or calculated in the Active Ag Fields. Every comparison test was re-run after excluding Active Ag Fields and Natural Wetlands to compare restoration age classes exclusively, but narrowing the comparisons in this manner did not change any significance results, so only the all-inclusive comparison results are shown.
3.6.3 Refined chronosequence analyses

I also hypothesized that, in WRP sites, plant community characteristics and soil properties would change gradually with years restored (as opposed to age class) (see H₂, Section 2.5). With the remaining hypotheses, I suggested that these temporal changes are influenced by land-use history (H₃) and the zone from which the measurements were taken (H₄) such that temporal changes are different between post-tillage restorations and post-non-tillage restorations and different among meadow, emergent, and open-water zones. To address this, I tracked response variables over several chronosequences. I say “several chronosequences” rather than “several analyses of a single chronosequence” primarily because separating analyses based on land-use history produced fundamentally different data series. That is, post-tillage restorations and post-non-tillage restorations cover different timelines (thus, constitute different chronosequences). So, this multiple chronosequence approach allowed me to investigate the effect of years restored in addition to two other factors that can influence post-restoration dynamics: prior land-use and zone type.

The prior land-use factor had three levels or categories to which sites were assigned: (1) tilled ag fields, (2) untilled ag fields, and (3) all ag fields. Analyzing chronosequences that only included either previously tilled or untilled sites allowed me to isolate the effects of land-use history/pre-
restoration condition while the chronosequences that included all sites were used to test hypotheses regarding all WRP sites.

Observations from each site were from (1) the meadow zone, (2) the emergent zone, or (3) the open water zone, or are (4) whole-site averages, so the factor of zone type included four levels. Regressions of whole-site averages were designed to detect changes as they occurred on all land enrolled in the WRP. Regressing zone-specific observations was done to track changes in specific habitat types within WRP sites, as they may follow distinct successional trajectories and/or soil development patterns. In summary, the chronosequences followed a 3 × 4 factorial design in that they collectively took on all possible combinations of prior land-use and zone type, resulting in analyses that ranged in scope from narrow (using only sites with particular land-use histories and/or only data from a particular zone type) to very broad (disregarding specific land-use histories and only considering site-level data).

Simple linear regressions were used to detect significant relations between response variables (log-transformed as needed) and years restored across all chronosequences. Linear relations were considered significant at \( \alpha = 0.05 \), though marginally significant relationships in which \( 0.5 < P < 0.1 \) are also presented to allow discussion of the age-related trends that may be statistically weak, but ecological important. When significant (or, in some
cases, marginally significant) age-related trends were detected for a given variable, I calculated recovery times using each relation’s respective linear regression equation and data from comparable reference sites [recovery time = ($x_{\text{natural wetlands}}$ + y-intercept) ÷ line slope]. Recovery times were defined as the number of years following restoration at which a parameter in restored wetlands matched that of the average natural wetland. Recovery times were not calculated for regressions that were insignificant or sloped in the wrong direction relative to the natural wetland reference points, but recovery times were calculated for some marginally significant relations. All statistical procedures were performed using SPSS 19 (IBM Corp, Armonk, NY, USA).

4. RESULTS

4.1 GENERAL LAND-USE HISTORY COMPARISONS

4.1.1 General Land-use History Comparisons – Belowground Variables

No significant differences were found among Active Ag Fields, Young Restorations, Middle-age Restorations, and Old Restorations with respect to any belowground variable, including gravimetric and proportional measures of SOM (Fig. 3). Soils in all restoration age classes were similar to each other and were, on average, indistinguishable from active croplands and pastures. Natural wetlands were distinct from all other land-use groups in terms of SOM
(Fig. 3.a-b), bulk density (d), and soil moisture (e), but not in terms of PMC, which was statistically equal among all land uses (Fig. 3.c).

Among the restoration age classes, Middle-age Restorations had the highest fine root biomass (Fig. 4.a) and were unique in that they were comparable to Natural Wetlands. In terms of coarse root biomass, all restoration age classes ranked equally and as intermediaries between Active Ag Fields and Natural Wetlands (Fig 4.b). Rhizome biomass (Fig. 4.c) and TBPB (Fig. 4.d) were found in similar quantities among the agricultural and restoration sites, and both measurements showed all restored wetlands to be deficient relative to Natural Wetlands.

4.1.2 General Land-use History Comparisons – Belowground Changes

The belowground environments of restored wetlands were expected to diverge from their former agricultural condition as they aged so that the proportional differences between each wetland and its corresponding ag field would be greater for older wetlands. I found that the amount of divergence (change) in belowground variables did not vary significantly among restoration age classes (Fig. 5, 6).

Yet, percent changes in SOM, while statistically similar among the restoration age classes, showed some noteworthy patterns. Gravimetrically, SOM changes became slightly more positive from Young to Old Restorations,
indicating modest SOM gains (Fig. 5.a). In the average Old restoration, SOM increased in weight by 24%. However, this gain was not enough to distinguish Old sites from Young and Middle-age sites statistically nor was it enough to make Old sites comparable to Natural Wetlands (which had an average of 233% more grams of SOM than their corresponding ag fields).

Another notable, although less consistent pattern was observed for changes in percent SOM (Fig. 5.b). Change in percent SOM was negative for Young Restorations but became more negative (although not significantly so) in Middle-age Restorations, before shifting to a positive change (SOM gain) of 13% in Old Restorations. With this gain, Old Restorations were statistically comparable to Natural Wetlands. Still, each natural wetland had approximately 200% more SOM by weight than the corresponding ag field (Fig. 5.a).

Percent change in PMC did not show a consistent or significant change from Young to Old Restorations (Fig. 5.c). The difference in PMC between Natural Wetlands and their corresponding ag fields was highly variable, but was, on average, not distinctly greater than any restoration age class. This seems to align with Fig. 3.c, which shows little difference between the PMC pools in wetland sites and those of active ag fields.
Percent change in bulk density did not vary significantly among the restoration categories (Fig. 5.d) but showed an inconsistent pattern similar to that of percent SOM. Soils in the oldest WRP sites experienced the greatest decrease but were not yet representative of Natural Wetlands. WRP soils typically had higher moisture contents than their agricultural counterparts (had positive changes) but were consistently drier than any natural wetland (Fig 5.e).

Post-restoration fine root biomass was slightly greater in Middle-age and Old Restorations than in Young Restorations but was statistically similar among all age classes (Fig. 6.a). Percent change in TBPB was generally very high (many WRP sites exceeded their adjacent ag fields by 500% by weight,) but did not vary be age class (Fig. 6.b).

The lack of coarse root and rhizome biomass in ag fields made it difficult to calculate meaningful measures of percent change (the calculation requires non-zero values for the ag fields). Thus, I omitted percent change in coarse root and rhizome biomass from the General Land-use History Comparisons. However, these measurements were incorporated in the comparisons of TBPB because TBPB included coarse root and rhizome biomass in addition to fine root biomass.
4.1.3 General Land-use History Comparisons – Aboveground Variables

Only restored and natural wetlands were included in comparisons of aboveground variables, as these variables were not measured in the ag fields. Site-level calculations of mean water depth in WRP and natural wetlands were consistently low (Fig. 7), as only small portions of these wetland sites had standing water at the time of sampling. This result contrasted with that of soil moisture in that, while WRP sites had slightly more standing water than Natural Wetlands, they had significantly drier soils (Fig. 5.b).

A slight increasing trend in LAB was found from Young to Old sites, but increases were not significant (Fig. 8.a). Litter mass also increased modestly by ~120 g m$^{-2}$ from Young to Old Restorations, but to the point that Old sites were statistically comparable to Natural Wetlands, which averaged 517 g m$^{-2}$ (Fig 8.b). In WRP restorations, TAB was lower than that in Natural Wetlands (900 g m$^{-2}$), but statistically similar to them (Fig. 8.c).

Vascular plant richness varied marginally ($P = 0.057$) and were generally lowest in Natural Wetlands (Fig. 9.a) which were less rich, presumably due to community dominance by one or few cattail species (Typha spp.). Modified Shannon indices of vascular plant diversity showed a
very similar pattern (Fig. 9.b), but differences between natural and restored wetlands were less pronounced ($P = 0.241$).

While significant differences among the restoration age classes were rare, the patterns of change in relative vegetative cover from Young to Old Restorations varied among life-form categories. Graminoid cover was relatively high in Young Restorations but peaked in Middle-age sites before declining in Old sites (Fig 10.a). Natural Wetlands had more graminoid cover than any restoration group, but this was likely because these sites were mostly Typha-dominated marsh habitats. Forb cover was similar among the land-use history categories but increased from Young to Old sites (Figure 10.b). Natural Wetlands had the most tree seedling/shrub cover (Fig 10.c). These plants were extremely scarce in Young sites but were not significantly more abundant in older restorations. Average cover of submersed and floating aquatic plants increased significantly from ~4% to ~25% from Young to Old Restorations (Fig 10.d). However, ~25% coverage far exceeded that of Natural Wetlands, which were, in fact, more comparable to Young Restorations. Algae, bryophytes, and ferns occurred in less than 40% of sampling quadrats, so these life-form groups were omitted from these comparisons to avoid analyzing zero-inflated datasets.

Although differences among site categories were only marginally significant ($P = 0.067$), relative cover of obligate wetland plants in restored
wetlands increased and approached cover estimates of *Natural Wetlands* over time (Fig 11.a). This type of consistent pattern was unapparent for facultative wetland species, but cover for these wetland plants was, on average, slightly greater in *Natural Wetlands* (Fig. 11.b). Cover of facultative plants showed more, albeit insignificant variation within and among the categories (Fig. 11.c). *Natural Wetlands* had little facultative upland plant cover (Fig. 11.d) and were omitted from comparisons of upland plant cover because such species were not found (Fig. 11.e), but all restoration age classes were similar in these regards.

Relative cover of annuals consistently decreased from Young to Old Restorations (Fig. 12.a), while cover of perennials increased (Fig. 12.b) although changes were slight. Yet, perennial cover was significantly greater in *Natural Wetlands* compared to Young Restorations. Biennial species were not observed in *Natural Wetlands*, and cover estimates were not different among the restored wetland categories (Fig. 12.c).

Cover of documented invasive plants did not vary among the restoration age classes (Fig. 13). Interestingly, *Natural Wetlands* had significantly more invasive cover than most WRP sites (only Middle-age Restorations were statistically similar). This pattern was seemingly driven by invasive cattail species, which accounted for more than 30% of total plant cover in *Natural Wetlands*. 
4.2 REFINED CHRONOSEQUENCE ANALYSES

4.2.1 Refined chronosequence analyses – Belowground Variables

Regressing each response variable over years restored (site age), then separating regressions based on prior land-use and/or zone type (see Section 3.10.3) resulted in several hundred chronosequence analyses. Each response variable was subject to 12 unique regressions so that soil and plant changes could be tested and compared among entire sites, specific zone types, and different land-use-history classifications.

Variation in SOM (g m\(^{-2}\) and %) could not be explained with years restored, even while controlling for prior land-use and zone type. So, no significant or marginally significant trends were detected using SOM measurements across any of the 24 unique chronosequences (*data not shown, but see Section 4.2.2*). This was also true of PMC. Soil moisture and coarse root biomass were the only belowground variables to change significantly. Still, these patterns were not broadly detected.

At the whole-site scale, and only across a chronosequence consisting of untilled sites, soil moisture increased linearly from ~23% to ~39% (Fig. 14.a), so that soil moisture in the oldest restoration site (15 years old) was only 24% less than the average moisture content of natural wetland soils. Using the recovery time equation in Section 3.10.3, I calculated that, if
increases remained linear, WRP sites with no history of tillage can be expected to attain "natural levels" of soil moisture by the age of 37 years.

Coarse root biomass increased in the meadow zones of all sites (Fig. 14.b) but did not show a pattern when tilled and untilled sites were considered separately. Coarse root biomass was low (near 0 g m\(^{-2}\)) in the youngest sites but was comparable to or exceeded natural levels (318 ± 44 g m\(^{-2}\)) in the oldest restorations. The linear regression of the increase suggests that coarse root biomass in the average WRP meadow zone will match the average natural wetland after being restored for 20 years.

Bulk density displayed a marginally significant change (\(P = 0.054\)), but this decreasing pattern was only detected at the whole-site scale and only in sites that were never tilled (Fig 14.c). The linear regression estimated that untilled WRP sites would have natural wetland soil densities (~0.5 g cm\(^{-3}\)) within 27 years

4.2.2 Refined chronosequence analyses – Belowground Changes

Each belowground change datum was a percent change value between a (proxy) pre-restoration value and a post-restoration value. As such, belowground change values were expected to be near zero for very young sites (as they have had little time to develop away from the pre-restoration condition) then become greater as sites become older (producing
a linear relationship between belowground change and years restored). No significant trends were detected using SOM measurements. However, at marginal significance, percent change in SOM (g m\(^{-2}\)) and SOM (%) increased with years restored in meadow zones of sites that were once tilled (Fig 15). The peripheral (meadow) zones of natural wetlands had an average of 212% more SOM (g m\(^{-2}\)) and 440% more SOM (%) than their corresponding tilled ag fields. Assuming linear increases, it would take the meadow zones of WRP sites nearly 47 years on a weight basis (Fig 15.a) and 74 years on a percent basis (Fig. 15.b) to match this degree of difference.

Percent change in PMC showed no trends across chronosequences with data from formerly tilled sites or data from emergent and open-water zones, but showed a marginally significant increase across a chronosequence consisting of meadow zones that were restored from non-tillage agriculture (Fig. 15.c). These restoration zones had less PMC than their corresponding ag fields, suggesting that PMC declined immediately after restoration. At the observed rate, it would take 20.1 years for restored meadows to recover from the post-restoration losses (return to agricultural or baseline levels) and 245 years to attain a natural wetland condition.

Very few other belowground metrics (most relating to belowground plant biomass) showed marginally significant relationships, but had extremely
low $R^2$ values (all < 0.1; data not shown). All other measurements did not relate to years restored.

**4.2.3 Refined chronosequence analyses – Aboveground Variables**

Eighteen significant relations were detected between years restored and various aboveground plant variables. These are summarized in Table 2, and select relations are presented additionally as scatter plots. Relations were restricted to variables concerning cover by certain life-forms and life-cycle durations, aboveground biomass fractions, and vascular species richness. Among these, the spatial and temporal aspects of recovery were highly variable. Thirteen of the significant regressions were zone-specific (related only meadow, emergent, or open-water zone data) and/or showed changes across sites with a particular land-use history. The remaining five were detected using site-level data from both tilled and untilled sites. Eleven regressions suggested floristic recovery within 15 years after restoration. In these cases, recovery was observed within the time-frames of this study’s chronosequences, and recovery times were not calculated based on extrapolated regression lines.

Cover of forbs recovered within a year across some chronosequences. Cover of submersed/floating aquatic plants also achieved natural wetland levels within in a year, yet this was partly explained by the fact that natural
wetlands had very little submersed/floating plant cover. Vascular plant species richness also recovered rapidly (Fig. 16.a). At year 0, whole sites and emergent zones restored from tillage had very low richness (averaging ≥ 1 species/m$^2$). By year one, these sites and zones had higher richness values than all reference wetlands (which averaged > seven species/m$^2$) meaning that recovery occurred within months of being restored. Five additional chronosequences showed that cover of forbs (Fig. 16.b), aquatic plants, annuals, and perennials matched their respective natural reference points within 15 years. Interestingly, all chronosequences that indicated recovery within 15 years also showed their response variables “overshooting” their natural reference points; these measures of plant biomass, cover, and richness approached the average natural wetland condition but then continued to increase or decrease.

Annual plant cover was among the variables to overshoot its natural reference point and was also the only aboveground variable to decrease (instead of increase) as a function of site age (Fig. 16.c). The peripheral zones of natural wetlands had few annual plants (accounting for ~5% of total plant cover). It took only eight years for WRP meadows to drop from ~11% to 5%. A drop to near 0% occurred during the next seven years.

Cover of tree seedlings and shrubs, along with litter mass and TAB, did increase with time across select chronosequences but did not reach natural
levels within 15 years. Thus, recovery times were based on extrapolated regression lines. At the whole-site scale in sites that were never tilled, litter mass is expected to reach natural levels (517 g m\(^{-2}\)) by year 24. In the emergent zones of natural wetlands, litter is more abundant (751 g m\(^{-2}\)). It would take more than twice as long (52.7 years) for the emergent zones of WRP sites to match the emergent zones of natural wetlands in this regard (Fig. 16.d). Cover of tree seedlings and shrubs in WRP meadows is projected to take nearly as long (52.1 years).

The open-water zones of previously tilled restoration sites showed a significant change in submersed/float aquatic plant cover. Within 14 years, these plants increased from ~0% to ~30%, but I was unable to calculate a recovery time because natural wetlands lacked zones that were comparable to the open-water zones of WRP sites (see Section 3.3). Mean water depth, modified Shannon index values, and cover of invasives did not show age-related trends across any chronosequence. Cover of all five WIS groups also failed to change as a function of years restored.
5. DISCUSSION

5.1 GENERAL LAND-USE HISTORY COMPARISONS

5.1.1 Restored soils are similar to agricultural soils

General Land-use History Comparisons addressed my first hypothesis (H₁) that SOM concentrations and other measurements varied among sites with different agricultural/restoration histories (see Section 2.5). Study sites were grouped based on agricultural activity and/or years restored. Active Ag Fields are systems that were currently and continuously being impacted by agriculture, while Natural Wetlands exemplified habitats that were never directly modified for agricultural purposes. Therefore, the sites that comprised these two categories represented opposite extremes on a continuum of agricultural disturbance, a potent driver of ecosystem change (Matson et al. 1997). Interestingly, few studies use both ag fields and natural wetlands as reference sites even though historical agricultural conversion is a major provocation for wetland restoration (Gleason et al. 2008, 2009).

As retired ag fields that have since been restored, WRP sites were classified as intermediaries on this continuum but were split further based on years restored (which can also be interpreted as the number of years without agricultural disturbance or the number of years allowed to recover from such disturbances). Comparisons pointed to two interrelated conclusions regarding
ecosystem development within WRP sites: restored WRP sites are often more similar to active ag fields than to natural wetlands with respect to belowground variables and WRP sites of different age classes are generally indistinguishable from each other. At the time of sampling, WRP restorations had not produced soils that were physicochemically or rhizospherically distinct from ag land, regardless of age class (Fig. 3, 4).

Such deficiencies in SOM, root/rhizome biomass, and soil moisture and excessively high soil densities relative to natural wetlands could indicate permanent agricultural alteration. Dexter and Zoebisch (2006) speculated that intense agricultural disturbances could push soil systems past critical thresholds beyond which typical functions such as C accumulation could not resume. In these cases, soil properties like SOM content would remain at or near their agricultural states, even after agricultural activities have been discontinued. An alternative interpretation is of slow recovery, rather than no recovery. Ballantine and Schneider (2009) studied a comparable set of wetlands restored under a state program in an overlapping region of New York and found SOM accretion and other soil properties to change slowly during the first decades after restoration. They offered three explanations that might pertain to the WRP sites of this study.

First, landscape/hydrogeomorphic factors might have limited certain aspects of soil development. The restoration sites used in my study were
constructed as small, depressional wetlands that were to exist as discrete patches within predominantly agricultural landscapes. Sites were surrounded entirely by non-wetland land cover types (e.g., mesic ag land, upland meadow or hedgerow) and lacked surface water connections with adjacent ecosystems. They met the definition of “geographically isolated wetlands” put forth by Tiner (2003) because they are deprived of many of the external water-, sediment-, and biotic material-inputs that other wetland types receive. Without these allochthonous inputs, SOM formation and accumulation cannot occur as fast as it does in other, more “open” wetlands systems such as restored salt marshes (Craft et al. 2002), restored mangrove swamps (Osland et al. 2012), and restored riparian wetlands (Mitsch et al. 2005), which receive energy and materials via tidal pulses or other flooding events.

Second, the plant communities that occupied restoration sites for the first several years following restoration may not have been contributing much OM to the underlying soil systems. However, the OM supplies may not have been low as plant biomass returned to natural levels within 15 years (Fig. 8). The reason SOM stocks did not recover concurrently with plant biomass stocks is not clear, but a similar discrepancy was found by Cole et al. (2001). They offered a partial explanation involving hydrologic SOM exporting, but this would only apply to “open” systems and not to more isolated WRP sites.
Another explanation by Cole et al. (2001) brought up the issue of litter quality. Litter quality is determined by tissue chemistry which varies substantially even among wetland species (Hume et al. 2002). The plants that dominated my restored study sites for the first 15 years may have produced highly decomposable litter, which is more likely to be lost before entering long-term storage as SOM (Atkinson and Cairns 2001). I did not measure any indicator of litter quality or decomposition rate for this study, but I did track the relative abundance of several qualitative plant traits (life-form, WIS, life-cycle duration, and invasiveness), which are sometimes linked to litter quality/decomposability (Pérez-Harguindeguy et al. 2000) and certain aspects of C cycling (Gill and Burke 1999). Very few trait-based plant groups changed significantly or consistently from Young to Old Restorations (Fig. 10-13), which would support the notion that WRP plant communities did not experience the qualitative or functional changes necessary to promote increases in SOM.

The discrepancy could also be due to a multi-year delay between plant production and SOM accumulation (as in an ecosystem time-lag). The conversion of plant litter to SOM, as it occurs in realtime, is not well-understood. So, it is conceivable that actual changes in SOM levels happen years after a site first meets the conditions necessary for SOM changes. This would align with recent syntheses that have reaffirmed that floristic parameters (biomass production, community composition, etc.) are indeed
tightly coupled with soil and belowground variables (Bardgett and Wardle 2010), but not necessarily on the same time-scales. If time lags are inherent in the plant biomass-to-SOM conversion process, they would be more apparent in the restorations of this study (compared to others) because they are isolated and not significantly subsidized with energy/materials from other ecosystems.

Third, restoration methodologies may have compelled on-site soils to retain a more agricultural condition (high bulk density, low OM concentrations). Although WRP projects are technically restorations, they usually require earth moving and water additions on a scale more evocative of wetland creations (constructions of wetlands on sites that never were wetlands). Heavy machinery is used extensively to excavate basins, build embankments, etc. (WRP contract holders, NRCS staff, personal communication). Such machinery may be necessary to revert entire ag fields to wetlands but can also unintentionally impact soil properties, including aggregate structure (Elliot 1986, Tisdall and Oades 1980), texture (Brady and Weil 1999), and bulk density (Schaffer et al. 2007).

Bulk densities in WRP sites of all ages, for example, were on par with Active Ag Fields and were approximately three times greater than Natural Wetlands (Fig. 3.c); this may be explained simply by the persistent effect of soil compaction by heavy machinery traffic (Nair et al. 2001, Campbell et al.
2002, Hossler and Bouchard 2010) (*but see also* Section 5.3.1 *for remarks on the effects of engineered clay layers in the low-elevation zones*). In this study, bulk density was of interest because of its negative relation with SOM concentrations in restored wetlands (Meyer *et al.* 2008). Adding SOM to any volume of soil can decrease bulk density, but high densities may *first* impair SOM accumulation by interfering with root growth (Lal and Kimble 2001, Dexter and Zoebisch 2006). This can then hinder the stabilization (Six *et al.* 2000) and vertical distribution (Ballantine *et al.* 2012) of OM. This study’s root biomass data pertained only very generally to the top 20 cm of soil, but it is possible that most roots were restricted to the top 5-10 cm and that OM deposition beyond that depth was scarce, leaving most of what I considered the “topsoil” devoid of OM.

### 5.1.2 Weak evidence of ecosystem development

With increasing age class, WRP sites were expected to show divergence from their previous agricultural condition (become increasingly dissimilar to ag fields) *and* convergence on the presumed natural condition (directionality toward the average reference wetland). This would mean that, of all restorations, *Young Restorations* would be the most similar to *Active Ag Fields* and *Old Restorations* would be the most similar to *Natural Wetlands*. I found that belowground variables followed this hypothesized pattern more closely when expressed as belowground changes.
Belowground change data were (1) *relative* to a unique pre-restoration quantity and (2) were *proportional* measures. Each site’s belowground change value was *relative*, in that I paired each wetland site with an active ag field. Each ag field was closely related to its corresponding wetland site in terms of geography, topography, and land-use history and thus, was the best available proxy for true baseline data (which may also be referred to as “pre-restoration” or “agricultural” data). To date, few studies have attempted to ascertain such data using paired site study designs (*but see* Gleason *et al.* 2008, 2009) even though many wetland restorations are, at their core, attempts to revert ag lands back to wetlands. Expressing the data as *proportional* (percent) changes removed some of the error associated with using absolute values. Absolute values of SOM content in restoration sites, for example, are inextricably tied to pre-restoration and pre-agriculture levels, which can vary substantially among sites and can obscure the effect of *age class*. This issue might have played out in a very similar study by Besasie and Buckley (2012), which found a weak temporal trend in SOM concentration (g kg\(^{-1}\) of soil) but no patterns in SOM content (g m\(^{-2}\)).

The relative and proportional nature of the belowground change data helped to standardize the soil and belowground metrics used to assess recovery. I contend that, with standardization came enhanced comparability among sites (an important consideration in chronosequence studies; *see* Section 2.4), and with enhanced comparability came a decreased chance of
making Type I errors regarding positive soil development across the age classes. To this, I attribute the fact that I found percent changes in SOM to follow the hypothesized temporal patterns more closely (compared to absolute measures of SOM), such that percent change in SOM (%) in Old Restorations became statistically comparable to the condition of Natural Wetlands (Fig. 5.b).

If percent changes in SOM are to be taken as more accurate depictions of SOM dynamics, then it should also be noted that these metrics showed that WRP soils initially experienced SOM losses (Young and Middle-age Restorations had negative percent changes) before experiencing SOM gains as they became Old Restorations. Losses in the younger sites were perhaps artifacts of the physical disturbances incurred during the earth-moving phases of restoration (Shaffer and Ernst 1999, Hossler and Bouchard 2010), as physical soil disturbance is generally known to promote SOM loss (see Section 2.2). The shift from SOM loss to SOM gain between Middle-age and Old age brackets seems to indicate a general threshold age of 10-15 years, beyond which soils can finally begin to sequester more C than they release.

Soil PMC, bulk density, and moisture dynamics were also slightly more as hypothesized when expressed as percent changes. Restored soils had gained PMC, decreased in density, and became wetter relative to their
agricultural baselines by the time they could be considered Old (Fig. 4.c-e). However, the changes from Young to Old Restorations were statistically negligible, and in the case of bulk density and moisture, did not bring restored soils up to par with natural wetland soils. It is possible that bulk density is more resistant to change; Froehlich et al. (1985) found that soil bulk density returns to natural levels very slowly in compacted forest skid trails. Parameters such as soil PMC and moisture, which represent relatively unstable components of soil, may vary on short timescales and, therefore, show no steady inter-annual trends. Bruland and Richardson (2005), for example, found significant monthly fluctuations in soil moisture in a restored wetland in North Carolina.

5.2 REFINED CHRONOSEQUENCE ANALYSES

5.2.1 Conditions throughout restoration sites may not favor carbon storage

Significant ($P < 0.05$), positive relations between years restored and SOM content were to be interpreted as evidence of SOM accumulation (belowground C storage). In effect, SOM dynamics were analyzed over 48 different scenarios, each of which considered a particular measurement of SOM (expressed either gravimetrically or as a percentage, and as either a belowground variable or a belowground change), for a particular group of sites (those restored from tillage, non-tillage, or both sensu my fourth
hypothesis), in a particular portion of a restoration site (one or all zones *sensu* my third hypothesis),

Significant relationships were not detected in any scenario, which suggests that significant SOM gains do not occur within the first 15 years following restoration. This conclusion aligns with those drawn from the less refined chronosequences of the *General Land-use History Comparisons* and those of similar studies (Shaffer and Ernst 1999, Ballantine and Schneider 2009, Besasie and Buckley 2012). However, these regression results showed that this conclusion universally applies to sites restored from both tillage and non-tillage (falsifying my third hypothesis of tilled sites accumulating SOM more rapidly than untilled sites) and to all zones (falsifying my fourth hypothesis which postulated SOM accumulation differences among the habitat zones). The lack of SOM accumulation across all zone types could be generally explained by the fact that primary production was matched or exceeded by respiration (SOM inputs ≤ SOM outputs). Yet, the underlying reasons, either “unnaturally” low production or “unnaturally” high respiration, could vary by zone type (excluding the possibility of ecosystem time-lags; see Section 5.2.1).

In meadow zones, I suspect that the failure to gain SOM with age was due to excessively high rates of decomposition (high OM outputting) relative to natural wetlands rather than to low productivity (low OM inputting). As the
highest elevation zones, WRP meadows were the most vulnerable to warming and drying and, hence, were most conducive to OM mineralization (Bruland and Richardson 2005). *In-situ* measurements of soil respiration were not taken during this study, but lack of standing water (Table 3) would support this claim by implying aerobic soils. The claim is also supported by higher soil PMC concentrations in this zone (Table 2). Soil PMC is not a direct substitute for *in-situ* measures of soil respiration (actual C output) but, holding all other field conditions constant, more PMC would indicate higher rates of respiration (Alvarez and Alvarez 2000).

Finding more PMC in the higher elevation portions of the WRP sites is, in some ways, inconsistent with Meyer *et al.* (2008), who measured potential C mineralization rates (g m\(^{-2}\) day\(^{-1}\)) and found them to be slightly lower for soil from higher elevation habitats (“margins”) of restored wetlands in the Platte River Valley (PRV) compared to lower elevation habitats (“sloughs”). However, “low” and “high elevation” habitats in PRV wetlands do not equate ecologically with “low” and “high elevation” zones of WRP sites (*i.e.*, WRP meadow zones are much higher than PRV margins and WRP open-water zones are much lower than PRV sloughs). Therefore, it is mostly inappropriate to draw analogies between PRV habitats and WRP zones.

There is also evidence that OM inputs were high in meadow zones (strengthening the arguments the high OM outputs, not low OM inputs, were
limiting SOM accumulation in these areas), but the evidence is not resolute. Finding all aboveground plant biomass fractions in WRP meadow zones to exceed those in analogous zones of natural wetlands (Table 4) indicates that there were adequate quantities of OM. On the other hand, root biomass fractions were considerably lower than in natural wetlands (Table 4). Rasse et al. (2005), without explicitly referencing wetlands, suggested that roots are often the dominant contributors to SOM pools, primarily because root tissues are more readily stabilized as SOM. Without well-developed rhizospheres, WRP meadows had less total non-woody plant biomass \( \bar{x} = 858 \text{ g m}^{-2} \) compared \( \bar{x} = 1329 \text{ g m}^{-2} \) in natural peripheral zones) and may or may not have had fewer stable OM inputs.

In open-water zones, less OM inputting clearly limited SOM accumulation. All plant biomass fractions were low (Table 4), and the average WRP open-water zone was sparsely vegetated. I attribute this to zone hydrology, which, in all wetlands, is a key forcing function (Niering 1985). Plots in open-water zones had, on average, 22 cm of standing water (Table 3), but some plots had near 70 cm, and water depths in the basin centers (although not recorded) were often deeper than 1 m. Additionally, these zones never experienced full drawdowns (NRCS staff, landowners, personal communication).
Deep, permanent water is a powerful environmental filter, one that selects against the germination/establishment/expansion of many plant species (van der Valk 1981, Kantrud et al. 1989). In certain cases, this filtering effect can constrain biomass production (Casanova and Brock 2000, Warwick and Brock 2003), which can only limit a system’s SOM accumulation potential. So, while it is extremely likely that these hydrologic conditions were inhibiting OM decomposition by sustaining anaerobic environments with negative redox potentials (Atkinson and Cairns 2001), they were simultaneously retarding OM production. This phenomenon was demonstrated and explained similarly by Shaffer and Ernst (1999), who found SOM concentrations in restored wetlands in Oregon to be lower in extensively flooded, open water sites.

In emergent zones, the lack of SOM sequestration is not as easily explained. These zones had standing water (although not nearly as much open-water zones; Table 3) and large quantities of plant biomass (more C influx; Table 4), and thus, ostensibly met the conditions necessary for SOM accumulation. However, SOM levels were generally lower than those in meadow zones (Table 4). A possible explanation could once again implicate “restoration methodology” and the inhibitory effect of high bulk density.

Creating high soil densities can be unintended consequence of using heavy machinery during restorations (see Section 5.2.1), but it is also done as
deliberate restoration technique. Water retention in restored or constructed wetlands can be realized by decreasing water outflow and/or by decreasing substrate permeability in areas meant to hold water (i.e., basins). It is advisable to reduce water seepage to below $10^{-6}$ cm sec$^{-1}$, and this is commonly accomplished by lining the basins with clay (Davis 1995). This was done in all WRP study sites by simply redistributing local pockets of clay-rich soil to the basins during the earth-moving phases. As a result, the emergent and open-water zone substrates had slightly higher bulk densities (Table 3) and, consequently, diminished SOM accretion properties (see Section 5.2.1). So, somewhat ironically in these cases, the immediate goal of water retention can conflict with the long-term goal of C storage.

5.2.2 Evidence of soil recovery is restricted to previously tilled meadow zones

As with the General Land-use History Comparisons, I report and discuss results of the Refined Chronosequence Analyses with significance values between 0.05 and 1 with the idea that they may be ecological significant and noteworthy (albeit to a lesser extent than results with significance values less than 0.05). Two, very specific SOM datasets shared marginally significant relations with years restored. Although $P$-values are high and $R^2$ values are low, I found percent change in SOM (g m$^{-2}$ and %) to increase in the meadow zones of restorations that were once tilled (Fig. 15).
Not finding even marginally significant relations in any other scenario implies two things.

First, the fact that the only SOM metrics to show even marginal significance were those expressed as “belowground changes” may reinforce the notion that relative/proportional measures of soil properties are most able to elucidate trends across a chronosequence (see Section 5.2.2). Second, that soils meeting certain conditions of prior land-use and zone type might be more suited for SOM accumulation than others. Tillage more efficiently depletes soil C than non-tillage agriculture (Kim et al. 2009), so it is likely that WRP sites restored from tillage had lower soil C stocks at the time of restoration. This cannot be confirmed without actual baseline data, but this study assumed that the ag fields paired with each wetland site approximated the pre-restoration condition of its respective wetland (see Section 3.1).

That said, tilled ag fields sampled for this study had, on average, 7.5% less SOM (g m\(^{-2}\)) than non-tilled ag fields (data not shown). It is then possible that restorations with histories of tillage had lower initial C stocks and, therefore, greater capacities to act as C sinks (high sink strength) compared to pastures and no-till croplands (Lal 2004, Smith 2004). When tilled fields are restored as WRP easements, the soils that underlay what become the meadow zones are subject to a unique blend of restoration techniques and ecological influences. Unlike emergent and open-water zones, meadow zone
soils were spared some the physical stresses of intentional densification during the restoration process (they were not expected to hold water). They also maintained moderately high rates of primary productivity. Perhaps, in meadow zones restored from tilled soils, greater soil C sink potential interacts with superior soil physical condition and the productivity of meadow plant communities to produce the highest C input to output ratios, ratios that are most likely to increase consistently with years restored.

5.2.3 Vegetational trends highlight broader issues in wetland restoration

Vegetation analyses, while not the focus of this study, returned the most positive results (95% of age-related trends detected during this study indicated vegetational changes rather than soil changes) and contributed to my overarching goal of assessing ecosystem recovery in New York's WRP sites. The observed plant structural and compositional changes highlight two broadly relevant topics in wetland restoration: (1) individual wetland restoration sites tend to be heterogeneous in terms of plant community structure and evaluations should consider these structural heterogeneities, as these imply functional heterogeneities, and (2) quantitative assessments of ecological recovery can be complicated by complex temporal patterns in indicator variables (i.e., “overshoots”) and tentatively-defined restoration targets.
Like naturally-occurring wetlands, wetland restoration sites often come to bear disparate habitat/plant community types within their boundaries (Seabloom and van der Valk 2003, Meyer et al. 2010). The occurrence, distribution, and overall nature of these habitats is dictated largely by site hydrogeomorphology (Seabloom et al. 2001, Hrivnák 2005), which in the case of New York’s WRP restorations, produces zones of open-water, emergent vegetation, and upland meadow. To my knowledge, the plant communities that define these zones (as they exist in west-central New York) have never been characterized, so I demonstrated that there are measurable differences among them (Tables 4-5).

During Refined Chronosequence Analyses, I tested for evidence of recovery in every plant community metric separately and in every zone separately (essentially testing if temporal differences accompany the spatial differences illustrated in Tables 4-5). I found that many metrics (e.g., obligate wetland plant cover) displayed no patterns of recovery, and of those that did, recovery was not detected across all zones (e.g., recovery of vascular plant species richness was detected in emergent zones but not specifically in the open-water or meadow zones; Table 2). This is evidence that these WRP restorations are not supporting all aspects of vegetative recovery but, more importantly, that open-water, emergent, and meadow zones evolve differently following restoration.
Few wetland restoration studies beyond this one (Craft et al. 2002, Gleason et al. 2008, Meyer et al. 2008, 2010) acknowledged or sought to compare the different zones, habitats, plant community types, etc., that can exist within individual restoration sites. This is in spite of the fact that variations in plant community structure/composition are expected to translate into variations in soil carbon storage (De Deyn et al. 2008) and many other ecosystem functions (Zak et al. 2003). So, after stratifying sampling among the zones, I showed that WRP properties in west-central New York are heterogeneous (containing substantial amounts of non-wetland habitat in addition to wetland habitat; Table 3) and that further investigations of total C stocks or any other aspect of ecosystem service provision in restored wetland should account for intra-site variability.

In addition to highlighting the issues of intra-site variability, vegetation analyses also highlighted the issue of “overshooting.” Six plant community metrics displayed “overshoot” patterns along one or more chronosequences (Table 2, Fig. 16.a-b). These metrics achieved equivalency to the average natural wetland but then deviated (continued to increase or, in the case of annuals cover, decrease) beyond natural wetland parameters. This phenomenon has been observed previously (Craft and Sacco 2003, Meyer et al. 2010) and obviously makes modeling and assessment less straightforward. In qualitative terms, this may be interpreted in two ways: (1) restorations are ecologically “on-track,” but recovery is not linear or direct
(Baldwin 2004) or (2) restorations are approaching novel states unlike the natural wetlands they were intended to replicate (Suding et al. 2004, Hobbs et al. 2009, Moreno-Mateo et al. 2012).

Neither interpretation can be verified without longer-term data. Furthermore, both interpretations rely on the establishment of an appropriate restoration target, a task often accompanied by an underappreciated amount of complexity. Natural systems used as reference sites are subject to significant inter-annual variations (White and Walker 1997, Landres et al. 1999). In the context of restoration, these variations mean that reference sites can actually be “moving targets” rather than static points of comparison (Christian et al. 2002, Meyer et al. 2010). Additionally, reference wetlands rarely (perhaps never) represent pristine systems (sensu Baldwin 2004). Although termed “natural,” all wetlands I used as references were found to be infested with invasive plant species (Fig. 13), namely *Typha angustifolia* L., *Lythrum salicaria* L., and *Phalaris arundinacea* L. This does not align with popular conceptions of “natural” and, therefore, constitutes an interesting caveat in discussions of restoration targets and recovery times. So, “natural” inter-annual variability and “unnatural” species assemblages in reference wetlands should be carefully considered in future studies of restored wetland development, or at the very least, prompt us to re-evaluate how post-restoration evaluations are conceptualized.
5.3 RECOMMENDATIONS FOR RESTORATION

While soil conditions (particularly SOM content and bulk density) directly or indirectly control the provision of several wetland ecosystem services, they are rarely given priority in wetland restoration planning (Shaffer and Ernst 1999). Whatever the underlying reasons or constraints are, this seems to be the case for many WRP wetlands of west-central New York. The results of this study suggest that, in those restorations, soil development towards a more “natural” wetland state has been impaired primarily by basic site conditions (basin geomorphology, water depth and distribution, and resulting zonation) and substrate preparation (intentional topsoil densification).

Many ecological outcomes of wetland restoration measures cannot be predicted precisely or are beyond control (Zedler 2000, Klötzli and Grootjans 2001, van Diggelen et al. 2001) but many basic site conditions are direct consequences of restoration methods. For example, the geomorphologies (the depth to which basins were excavated and the height to which embankments were constructed) of the WRP sites I studied were prescribed and shaped by NRCS practitioners. However, those geomorphologies often generated large areas of distinctly non-wetland habitat; embankments far above water level encouraged the development of upland meadow zones and basins with depths near or exceeding 1 m produced largely unvegetated
open-water zones, neither of which are conducive to SOM accumulation or other desirable wetland soil processes (see Section 5.2.1).

Zonation patterns including large proportions of upland meadow and open water could be prevented by (1) limiting the maximum height of embankments and maximum depths of basins relative to expected water depths and/or (2) reducing the grade between high- and low-elevations areas (Hollands 1990, Kentula 1992). This would minimize (without eliminating) topographic extremes and maximize the amount of emergent zone area with moderate water depths, thereby minimizing positive soil redox potentials (expected in the high-elevation meadow zones) and the vegetatively unproductive conditions (expected in the deeper open-water zones).

I suspect that correcting geomorphology (and resulting hydrology) would only be partially effective at promoting SOM gains if substrate preparation techniques continue to leave the uppermost soil layers relatively dense. This study associated the intentional densification of soil as it occurred during the lining of the basins with clay-rich soil with the general failure of WRP sites to accumulate SOM. Engineering impermeable soil layers is often the only feasible way to reduce to water seepage and ensure on-site water retention (Davis 1995), but this may simultaneously reduce SOM accumulation by restricting root growth and OM distribution (see Section 5.1.1). So, creating more emergent zone area by modifying geomorphology
would do little to promote SOM gains if this area is underlain by unsuitable substrates.

It is possible to augment the substrates that line WRP basins in ways that preserve water retention properties and promote SOM accumulation. Amending soils (i.e., adding exogenous C or OM) during restoration is thought to prime otherwise degraded soils for future OM production and accretion by decreasing soil density and improving soil nutrient status. In fact, amendments in the form of compost, biochar, straw, etc. have proven useful in stimulating C gain and other desirable soil changes (Sutton-Grier et al. 2009, Ballantine et al. 2012). In isolated depressional WRP restorations, a relatively easy and cost-effective option for amending basin substrates would be covering them partially or fully with pockets of intact topsoil (Davis 1995). Those soil amendments could be harvested and set aside prior basin grading and then added after grading is complete. Additionally, I contend that these would topsoil additions would not have to be organic soils to be effective at increasing emergent plant growth (many plants grow well on mineral soils) and could be still be effective if added many years after the restoration was implemented.

Finally, any efforts to promote SOM accumulation should be accompanied by efforts to quantify SOM accumulation. Measurements of SOM prior to restoration and then annually or biennially after restoration could
easily be incorporated into NRCS monitoring protocols given the affordability and simplicity of SOM analysis. As long as soil sampling is stratified by zone (as done in this study), holistic evaluations of SOM dynamics in WRP restorations could be accomplished, providing valuable insight into restored ecosystem functionality that could guide future restoration procedures. This would also decrease our reliance on chronosequence-based studies, which need to be formulated very carefully (as demonstrated by this study and others).

6. CONCLUSIONS

This study was a long-term (>10 year) examination of key structural and functional changes within wetlands restored under the WRP. As a federal wetland restoration program, the implicit goal of the WRP is to reintroduce functional wetland habitats to landscapes that have been modified by agriculture, such as those common to west-central New York. Yet, prior to this study, ecosystem dynamics within WRP sites have never been investigated in this region despite the program’s popularity (1,260 agreements and 21,404 hectares enrolled in New York between 1992 and 2011; USDA-NRCS 2011a). My analytical approaches aimed to test the assumption of ecosystem development (WRP sites becoming less like the active agricultural fields they are restored from and more like natural wetlands as they age).
Comparing Young, Middle-age, and Old Restorations to each other and against Natural Wetlands and unrestored Active Ag Fields showed that WRP soils, for the first 10-20 years, retain a very agricultural condition in terms of SOM concentrations and also soil PMC, density, and moisture. This aligns with previous studies of comparable wetland restorations (Shaffer and Ernst 1999, Ballantine and Schneider 2009, Besasie and Buckley 2012). Comparisons of soil variables in the form of belowground changes (which helped standardize soil data from different sites) also suggested that soils do not develop appreciably during the first 15 years post-restoration, but do cross a threshold at ~10 years, after which they begin gaining SOM.

Regressing WRP soil measurements over time, then refining regressions based on prior land-use and zone-type, revealed that SOM accumulation and other aspects of soil development (with few exceptions) do not proceed consistently toward natural conditions regardless of whether sites were restored from tillage or non-tillage agriculture and regardless of which zones types are considered. Yet, SOM datasets did show marginally significant temporal trends when expressed as belowground changes in the meadow zones of previously tilled sites, suggesting that some WRP soils are slightly more conducive to SOM accumulation than others.

Most evidence of ecosystem recovery was restricted to aspects of plant community composition and structure. Finding that vascular plant richness, cover of certain qualitative plant groups, and plant biomass fractions
approached natural wetland conditions allowed me to conclude that, in the WRP sites of west-central New York, there is a general incongruity between soil development and vegetational recovery and that plant community restoration is, in some regards, achievable within 15 years. Additionally, and unlike soil changes, vegetation changes seem dependent of land-use history and zone type (many of the patterns that suggested recovery were not found in both previously tilled and previously untilled restoration sites nor were recovery patterns found in all zones). This affirmed my suspicions that individual WRP sites harbor disparate habitats and these habitats function differently over time. However, my vegetation analyses also drew attention to some important considerations in evaluative wetland restoration research. One is that plant metrics “overshooting” restoration targets makes it difficult to determine/model recovery and choosing appropriate restoration targets is very often confounded by the fact natural systems are dynamic and virtually never meet all notions of “natural.”

For perspective, wetland attributes beyond physicochemical soil properties and plant community structures should be considered. Carbon storage (as crucial as it is) is not the only function wetlands can or should perform. Wetland functions also include habitat-related and hydrologic functions (see Section 2.1). It is conceivable that these non-biogeochemical functions can and have developed despite failures/delays in SOM accrual and other aspects of soil development. Furthermore, C storage is not an explicit
goal of the WRP nor is it a strong motivation for program enrollment (WRP contract holders, personal communication). However, even while acknowledging services not related to SOC/SOM, this study supports the assertion that restored wetlands are, at the most, partial compensations for historical wetland loss.
7. REFERENCES


Street, J. M. 1982. Changes of carbon inventories in live biomass and detritus as a result of the practice of shifting agriculture and the


8. TABLES
Table 1. Interpretative guide to Wetland Indicator Status. Interpretations and status designations of each species in the current study are adapted from and follow the PLANTS Database (United States Department of Agriculture, 2012). Provided as examples in parentheses are the species of each category found to be most common by the current study.

<table>
<thead>
<tr>
<th>Wetland Indicator Status</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Obligate Wetland</td>
<td>Almost always is a hydrophyte, rarely in uplands (<em>Typha angustifolia</em> L.)</td>
</tr>
<tr>
<td>Facultative Wetland</td>
<td>Usually is a hydrophyte but occasionally found in uplands (<em>Phalaris arundinacea</em> L.)</td>
</tr>
<tr>
<td>Facultative</td>
<td>Commonly occurs as either a hydrophyte or non-hydrophyte (<em>Juncus tenuis</em> Willd.)</td>
</tr>
<tr>
<td>Facultative Upland</td>
<td>Occasionally is a hydrophyte but usually occurs in uplands (<em>Lotus comiculatus</em> L.)</td>
</tr>
<tr>
<td>Obligate Upland</td>
<td>Rarely is a hydrophyte, almost always in uplands (<em>Symphyotrichum pilosum</em> (Willd.) G.L. Nesom)</td>
</tr>
</tbody>
</table>
Table 2. Floristic recovery in Wetlands Reserve Program (WRP) restorations in west-central New York, USA. Restorations followed conversion to cropland or pasture; sites were tilled ($n = 12$, ranging from 0-14 years old at the time of sampling) or untilled ($n = 5$, 0-15 years old) prior to restoration. Sampling (August-September 2010) was stratified by the habitat zones present at each site: meadow, emergent, and open-water zone (delineated and named according to hydrotopography/vegetation). WRP site parameters were tracked over several chronosequences to determine if they become more like reference sites (natural wetlands) with age. Chronosequences included sites with particular agricultural histories (tilled, untilled, or all sites) and considered particular areas of the sites (one zone type or whole sites). Shown are the only plant variables to change linearly with age, the chronosequence conditions in which these relations were detected ($\alpha = 0.05$), regression statistics, mean parameters of four natural wetlands (in the same units), and recovery time (the number of years following restoration at which WRP sites are expected to match the average natural wetland as determined by extrapolating regression lines).

1 Some variables matched natural conditions within the timeframe of the chronosequence then continued to increase or decrease (overshot). During instances of overshooting, it was not necessary to extrapolate regression lines to calculate recovery times.

2 Recovery times for open-water zone flora were not calculated as natural wetlands lacked distinct open-water zones.

<table>
<thead>
<tr>
<th>Floristic parameter</th>
<th>Agricultural history of sites included</th>
<th>Areas considered</th>
<th>Regression statistics</th>
<th>Natural wetlands</th>
<th>Recovery time (years)</th>
<th>Overshot†</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Richness of vascular, herbaceous plants and low-growing (≤ 1 m in height) woody plants</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of species per square meter</td>
<td>tilled</td>
<td>emergent zones</td>
<td>0.038</td>
<td>0.364</td>
<td>3.5</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td>No. of species per square meter</td>
<td>tilled</td>
<td>whole sites</td>
<td>0.041</td>
<td>0.354</td>
<td>6.0</td>
<td>&lt;0.1</td>
</tr>
<tr>
<td><em>Aboveground plant biomass fractions (grams per square meter) excluding tree leaves occurring ≥ 1 m above ground and woody tissues</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Living biomass</td>
<td>untilled</td>
<td>meadow zones</td>
<td>0.036</td>
<td>0.815</td>
<td>202.9</td>
<td>5.2</td>
</tr>
<tr>
<td>Litter mass</td>
<td>untilled</td>
<td>whole sites</td>
<td>0.002</td>
<td>0.976</td>
<td>517.1</td>
<td>24.1</td>
</tr>
<tr>
<td>Litter mass</td>
<td>untilled</td>
<td>emergent zone</td>
<td>0.022</td>
<td>0.864</td>
<td>750.6</td>
<td>52.7</td>
</tr>
<tr>
<td>Litter mass</td>
<td>all sites</td>
<td>whole sites</td>
<td>0.013</td>
<td>0.348</td>
<td>517.1</td>
<td>30.4</td>
</tr>
<tr>
<td>Living biomass</td>
<td>all sites</td>
<td>whole sites</td>
<td>0.048</td>
<td>0.236</td>
<td>883.6</td>
<td>30.3</td>
</tr>
<tr>
<td><em>Relative cover (%)</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forbs</td>
<td>tilled</td>
<td>emergent zone</td>
<td>0.041</td>
<td>0.356</td>
<td>6.7</td>
<td>8.2</td>
</tr>
<tr>
<td>Forbs</td>
<td>all sites</td>
<td>whole sites</td>
<td>0.029</td>
<td>0.281</td>
<td>17.2</td>
<td>0.9</td>
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<tr>
<td>Tree seedlings/shrubs</td>
<td>all sites</td>
<td>meadow zones</td>
<td>0.035</td>
<td>0.264</td>
<td>26.5</td>
<td>0.1</td>
</tr>
<tr>
<td>Floating/submersed aquatics</td>
<td>untilled</td>
<td>whole sites</td>
<td>0.001</td>
<td>0.982</td>
<td>2.9</td>
<td>1.6</td>
</tr>
<tr>
<td>Floating/submersed aquatics</td>
<td>tilled</td>
<td>open-water zones$^2$</td>
<td>0.049</td>
<td>0.355</td>
<td>n/a</td>
<td>n/a</td>
</tr>
<tr>
<td>Floating/submersed aquatics</td>
<td>all sites</td>
<td>whole sites</td>
<td>0.014</td>
<td>0.342</td>
<td>2.9</td>
<td>0.7</td>
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<tr>
<td><em>Annuals</em></td>
<td>untilled</td>
<td>meadow zones</td>
<td>0.012</td>
<td>0.908</td>
<td>4.6</td>
<td>7.6</td>
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<td><em>Perennials</em></td>
<td>untilled</td>
<td>meadow zones</td>
<td>0.019</td>
<td>0.878</td>
<td>89.8</td>
<td>8.3</td>
</tr>
<tr>
<td>Perennials</td>
<td>all sites</td>
<td>whole sites</td>
<td>0.020</td>
<td>0.312</td>
<td>95.8</td>
<td>17.8</td>
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<td>Perennials</td>
<td>all sites</td>
<td>meadow zones</td>
<td>0.040</td>
<td>0.252</td>
<td>89.8</td>
<td>10.8</td>
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</table>
Table 3. Physical properties of 21 active croplands/pastures, 17 Wetlands Reserve Program (WRP) restorations, and four natural, depressional wetlands in west-central New York, USA. Means and standard errors (SE) are shown by habitat zone (delineated and named by hydrotopography and vegetation). The WRP meadow and emergent zones correspond to the peripheral and emergent zones of natural wetlands, respectively. Natural wetlands lacked open-water zones. Zone areas and water depths were measured October 2010. Soil properties were derived from 20 cm-depth cores removed October 2010 and are also given as percent changes (quantifications of post-restoration change calculated using active croplands/pastures for proxy pre-restoration data; positive changes indicate increases/gains relative to comparable agricultural soils and negative changes indicate decreases/losses). Percent changes for natural wetland zones were calculated similarly though they were never converted to agriculture or restored.

<table>
<thead>
<tr>
<th>Physical characteristics</th>
<th>Cropland/pasture</th>
<th>WRP zone</th>
<th>Natural wetland zone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Meadow</td>
<td>Emergent</td>
<td>Open-water</td>
</tr>
<tr>
<td>Zone area (% of total site area)</td>
<td>Mean</td>
<td>n/a</td>
<td>45.1</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>n/a</td>
<td>4.1</td>
</tr>
<tr>
<td>Water depth (cm)</td>
<td>Mean</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>0.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

Soil properties

<table>
<thead>
<tr>
<th>Physical characteristics</th>
<th>Cropland/pasture</th>
<th>WRP zone</th>
<th>Natural wetland zone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Meadow</td>
<td>Emergent</td>
<td>Open-water</td>
</tr>
<tr>
<td>Organic matter (g m⁻²)</td>
<td>Mean 11875.0</td>
<td>14032.3</td>
<td>10366.8</td>
</tr>
<tr>
<td></td>
<td>SE   410.0</td>
<td>971.0</td>
<td>755.7</td>
</tr>
<tr>
<td>Organic matter (%)</td>
<td>Mean 4.2</td>
<td>5.6</td>
<td>3.9</td>
</tr>
<tr>
<td></td>
<td>SE   0.3</td>
<td>0.6</td>
<td>0.5</td>
</tr>
<tr>
<td>Potentially mineralizable carbon (g m⁻²)</td>
<td>Mean 723.1</td>
<td>741.5</td>
<td>585.4</td>
</tr>
<tr>
<td></td>
<td>SE   62.5</td>
<td>67.7</td>
<td>73.8</td>
</tr>
<tr>
<td>Bulk density (g cm⁻³)</td>
<td>Mean 1.4</td>
<td>1.2</td>
<td>1.4</td>
</tr>
<tr>
<td></td>
<td>SE   0.0</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Gravimetric moisture (%)</td>
<td>Mean 22.7</td>
<td>27.4</td>
<td>27.6</td>
</tr>
<tr>
<td></td>
<td>SE   1.2</td>
<td>1.9</td>
<td>1.9</td>
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</table>

Percent changes in soil properties

<table>
<thead>
<tr>
<th>Physical characteristics</th>
<th>Cropland/pasture</th>
<th>WRP zone</th>
<th>Natural wetland zone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Meadow</td>
<td>Emergent</td>
<td>Open-water</td>
</tr>
<tr>
<td>Organic matter (g m⁻²)</td>
<td>Mean n/a</td>
<td>21.4</td>
<td>-10.2</td>
</tr>
<tr>
<td></td>
<td>SE   n/a</td>
<td>10.7</td>
<td>8.3</td>
</tr>
<tr>
<td>Organic matter (%)</td>
<td>Mean n/a</td>
<td>41.7</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>SE   n/a</td>
<td>16.6</td>
<td>16.4</td>
</tr>
<tr>
<td>Potentially mineralizable carbon (g m⁻²)</td>
<td>Mean n/a</td>
<td>12.8</td>
<td>-5.8</td>
</tr>
<tr>
<td></td>
<td>SE   n/a</td>
<td>9.3</td>
<td>13.7</td>
</tr>
<tr>
<td>Bulk density (g cm⁻³)</td>
<td>Mean n/a</td>
<td>-9.0</td>
<td>1.3</td>
</tr>
<tr>
<td></td>
<td>SE   n/a</td>
<td>4.3</td>
<td>6.7</td>
</tr>
<tr>
<td>Gravimetric moisture (%)</td>
<td>Mean n/a</td>
<td>24.6</td>
<td>27.8</td>
</tr>
<tr>
<td></td>
<td>SE   n/a</td>
<td>8.7</td>
<td>9.8</td>
</tr>
</tbody>
</table>
Table 4. Vegetation parameters for 17 Wetlands Reserve Program (WRP) restoration sites and four naturally-occurring, depressional wetlands in west-central New York, USA. Means and standard errors (SE) are shown by habitat zone which were delineated visually and named according to topographic, hydrologic, and/or plant community indicators. The meadow and emergent zones of WRP sites experimentally corresponded to the peripheral and emergent zones of natural wetlands, respectively. Natural wetlands lacked distinct open-water zones. Fine root (< 2 mm diameter), coarse root (≥ 2 mm), and rhizome measures were derived from 20 cm-depth, 5 cm-diameter soil cores removed October 2010. Aboveground biomass was harvested August-September 2010 and excluded tree leaves occurring ≥ 1 m above ground and woody tissues.

<table>
<thead>
<tr>
<th>Cropland/Pasture</th>
<th>WRP zone</th>
<th>Natural wetland zone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Meadow</td>
<td>Emergent</td>
</tr>
<tr>
<td>Fine root</td>
<td>Mean</td>
<td>146.9</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>34.7</td>
</tr>
<tr>
<td>Coarse root</td>
<td>Mean</td>
<td>55.8</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>23.9</td>
</tr>
<tr>
<td>Rhizome</td>
<td>Mean</td>
<td>54.2</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>54.2</td>
</tr>
<tr>
<td>Living biomass</td>
<td>Mean</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>n/a</td>
</tr>
<tr>
<td>Litter mass</td>
<td>Mean</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>n/a</td>
</tr>
<tr>
<td>Total biomass</td>
<td>Mean</td>
<td>n/a</td>
</tr>
<tr>
<td></td>
<td>SE</td>
<td>n/a</td>
</tr>
</tbody>
</table>

Richness of vascular, herbaceous plants and low-growing (≤ 1 m in height) woody plants

<table>
<thead>
<tr>
<th>No. of species per square meter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
</tr>
<tr>
<td>SE</td>
</tr>
</tbody>
</table>
Table 5. Relative cover estimates (%) for select plant groups in 17 Wetlands Reserve Program (WRP) restoration sites and four naturally-occurring, depressional wetlands in west-central New York, USA. Means and standard errors (SE) are shown by habitat zone which were delineated and named according to hydrotopographic and/or plant community indicators. The meadow and emergent zones of WRP sites experimentally corresponded to the peripheral and emergent zones of natural wetlands, respectively. Natural wetlands lacked distinct open-water zones. Life-form, wetland indicator status, and life-cycle duration designations primarily follow the PLANTS Database (United State Department of Agriculture, 2012).

1Plant species were considered “invasive” if they were officially documented as being targeted by government plant control measures in New York or surrounding states (various sources) and may include native species.

<table>
<thead>
<tr>
<th>WRP Zone</th>
<th>Natural wetland zone</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Meadow</td>
</tr>
<tr>
<td><strong>Relative cover (%) of select plant life-forms</strong></td>
<td></td>
</tr>
<tr>
<td>Graminoids</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>SE</td>
</tr>
<tr>
<td>Forbs</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>SE</td>
</tr>
<tr>
<td>Tree seedlings/shrubs</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>SE</td>
</tr>
<tr>
<td>Submersed/ floating aquatics</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>SE</td>
</tr>
<tr>
<td><strong>Relative cover (%) by Wetland Indicator Status</strong></td>
<td></td>
</tr>
<tr>
<td>Obligate wetland plants</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>SE</td>
</tr>
<tr>
<td>Facultative wetland plants</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>SE</td>
</tr>
<tr>
<td>Facultative plants</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>SE</td>
</tr>
<tr>
<td>Facultative upland plants</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>SE</td>
</tr>
<tr>
<td>Upland plants</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>SE</td>
</tr>
<tr>
<td><strong>Relative cover (%) by life-cycle duration</strong></td>
<td></td>
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<tr>
<td>Annuals</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>SE</td>
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<tr>
<td>Biennials</td>
<td>Mean</td>
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<tr>
<td></td>
<td>SE</td>
</tr>
<tr>
<td>Perennials</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>SE</td>
</tr>
<tr>
<td><strong>Relative cover (%) of invasive plant species</strong></td>
<td></td>
</tr>
<tr>
<td>Invasive species</td>
<td>Mean</td>
</tr>
<tr>
<td></td>
<td>SE</td>
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</tbody>
</table>
9. FIGURES
Figure 1. Locations of 21 field sites in west-central New York, USA. All sites are proximal pairings of one wetland (restored or naturally-occurring) and one active agricultural field. Restored wetlands (n = 17) were non-tidal, depressional Wetlands Reserve Program (WRP; United States Department of Agriculture) sites restored between 1995-2010 following degradation by tillage (open circles) or non-tillage agriculture (cross-hatched circles). Naturally-occurring wetlands (black diamonds, n = 4) are depressional, Palustrine Emergent wetlands to which WRP sites were deemed most comparable.
Figure 2. Generalized Wetland Reserve Program (WRP: United States Department of Agriculture) easement with typical zonation pattern and example sampling locations. Easements under study were located in west-central New York, USA and restored from agriculture as non-tidal, depressional wetlands. Zones were delineated and named according to hydrotopographic and vegetational indicators. Sampling took place along three transects (solid black lines) which originated from the center of the open-water zone, extended to easement boundaries, and had random orientations (30°, 120°, and 225° shown as examples). Transects were sectioned by zone and 1 m² soil/plant sampling quadrats (black squares; not to scale) were placed on section mid-points so that each zone was sampled in triplicate.
Figure 3. Physicochemical properties (mean ± one standard error) of the top 20 cm of soil of 42 field sites in west-central New York, USA. Sites were sorted into five groups based on generalized land-use histories. Young, Middle-age, and Old Restorations were Wetlands Reserve Program sites restored from agriculture 0-3, 4-10, and 11-15 years prior to sampling (October 2010), respectively. Natural Wetlands (n = 4) are depressional, Palustrine Emergent. Active Ag Fields include 17 tilled and no-till croplands and pastures. Means were compared with One-way Analysis of Variance (df = 4 for all tests). Statistics generated using log-transformed data are marked with an asterisk (*). Statistically different groups are marked with different letters.
Figure 4. Belowground plant biomass fractions (mean ± one standard error) of the top 20 cm of soil of 42 field sites in west-central New York, USA. Sites were sorted into five groups based on generalized land-use histories. Young, Middle-age, and Old Restorations were Wetlands Reserve Program sites that were restored from agriculture 0-3, 4-10, and 11-15 years prior to sampling (October 2010), respectively. Natural Wetlands (n = 4) are depressional, Palustrine Emergent. Active Ag Fields include 17 tilled and no-till croplands and pastures. Statistics marked with a dagger (†) resulted from Kruskall-Wallis tests while all others resulted from One-way Analysis of Variance tests (df = 4 for all tests). Statistics generated using log-transformed data are marked with an asterisk (*). Statistically different groups are marked with different letters.

\[ F = 3.830, \ p = 0.011^* \]
\[ F = 35.165, \ P < 0.001^* \]
\[ H = 10.351, \ P = 0.035^† \]
\[ F = 15.511, \ P < 0.001 \]

\( TBPB \) (total belowground plant biomass)
Figure 5. Percent change in soil (0-20 cm) properties of 17 agricultural (ag) fields in west-central New York, USA since reversion to wetlands via the Wetlands Reserve Program (WRP). Young, Middle-age, and Old Restorations are WRP sites restored 0-3, 4-10, and 11-15 years prior to sampling (October 2010), respectively. Percent changes (mean + one standard error) are compared with One-way Analysis of Variance (α = 0.05) and were calculated for each WRP site relative to a paired ag field which provided proxy pre-restoration data (df = 3 for all tests). Included are mean differences between ag fields and Natural Wetlands (n = 4) to show how WRP soils are expected to change. Statistically different groups are marked with different letters.
Figure 6. Percent change in fine root and total belowground plant biomass (TBPB) (0-20 cm of soil) of 17 agricultural (ag) fields in west-central New York, USA since reversion to wetland sites under the Wetlands Reserve Program (WRP). Young, Middle-age, and Old Restorations are WRP sites restored 0-3, 4-10, and 11-15 years prior to sampling (October 2010), respectively. Percent changes (mean ± one standard error) are compared with One-way Analysis of Variance ($\alpha = 0.05$) and were calculated for each WRP site relative to a paired ag field which provided proxy pre-restoration data (df = 3 for all tests). Included are mean differences between ag fields and Natural Wetlands ($n = 4$) to show how WRP soils are expected to change. Statistically different groups are marked with different letters.
Figure 7. Water depth (mean + one standard bars) of 21 field sites in west-central New York, USA. Sites were sorted into four groups based on generalized land-use histories.
Young, Middle-age, and Old Restorations were Wetlands Reserve Program sites that were restored from agriculture 0-3, 4-10, and 11-15 years prior to sampling (October 2010), respectively. Natural Wetlands (n = 4) are depressional, Palustrine Emergent. Data were log-transformed before means were compared with One-way Analysis of Variance and found to be statistically similar.
Figure 8. Aboveground plant biomass fractions (mean + one standard error) of 21 field sites in west-central New York, USA. Sites were sorted into four groups based on generalized land-use histories. Young, Middle-age, and Old Restorations were Wetlands Reserve Program sites restored from agriculture 0-3, 4-10, and 11-15 years prior to sampling (August-September 2010), respectively. Natural Wetlands (n = 4) are depressional, Palustrine Emergent. Fractions exclude tree leaves occurring more than 1 m above the ground and woody tissues. Statistics marked with a dagger (†) resulted from Kruskal-Wallis tests, while all others are results of One-way Analysis of Variance tests (df = 3 for all tests). Statistically different groups are marked with different letters.

$^1$LAB (living aboveground biomass)
$^2$TAB (total aboveground biomass)
Figure 9. Plant community diversity metrics (mean + one standard error) for 21 wetlands in west-central New York, USA. Sites were sorted into four groups based on generalized land-use histories. Young, Middle-age, and Old Restorations were Wetland Reserve Program sites that were restored from agriculture 0-3, 4-10, and 11-15 years prior to sampling (August-September 2010), respectively. Natural Wetlands ($n = 4$) are depressional, Palustrine Emergent. Vascular plant diversity values are Shannon Index values ($H'$) modified so that "zero" values indicated no species present and "one" values indicated one species present. Statistics marked with a dagger (†) resulted from Kruskall-Wallis tests, while all others are results of One-way Analysis of Variance tests (df = 3 for all tests); groups means were not found to be statistically different.
Figure 10. Percent relative cover of select plant life-forms (mean + one standard error) in 21 wetlands in west-central New York, USA. Sites were sorted into four groups based on generalized land-use histories. Young, Middle-age, and Old Restorations were Wetland Reserve Program sites that were restored from agriculture 0-3, 4-10, and 11-15 years prior to sampling, respectively. Natural Wetlands (n = 4) are depressional, Palustrine Emergent. Statistics marked with a dagger (†) resulted from Kruskall-Wallis tests, while all others are results of One-way Analysis of Variance tests (df = 3 for all tests). Statistics generated using log-transformed data are marked with an asterisk (*). Statistically different groups are marked with different letters.
Figure 11. Percent relative cover of plants by Wetland Indicator Status (mean + one standard error) in 21 wetlands in west-central New York, USA. Sites were sorted into four groups based on generalized land-use histories. *Young*, *Middle-age*, and *Old Restorations* were Wetlands Reserve Program sites that were restored from agriculture 0-3, 4-10, and 11-15 years prior to sampling, respectively. *Natural Wetlands* (n = 4) are depressional, Palustrine Emergent. Statistics marked with a dagger (†) resulted from Kruskall-Wallis tests, while all others are results of One-way Analysis of Variance tests. Groups were not found to be significantly different.
Figure 12. Percent relative cover of plants by life-cycle duration (mean + one standard error) in 21 wetlands in west-central New York, USA. Sites were sorted into four groups based on generalized land-use histories. Young, Middle-age, and Old Restorations were Wetlands Reserve Program sites that were restored from agriculture 0-3, 4-10, and 11-15 years prior to sampling (August-September 2010), respectively. Natural Wetlands \( n = 4 \) are depressional, Palustrine Emergent. marked with a dagger \( (†) \) resulted from Kruskall-Wallis tests, while all others are results of One-way Analysis of Variance tests. Statistically different groups are marked with different letters.
Figure 13. Percent relative cover of invasive plant species (mean + one standard error) in 21 wetlands in west-central New York, USA. Sites were sorted into four groups based on generalized land-use histories. Young, Middle-age, and Old Restorations were Wetlands Reserve Program sites that were restored from agriculture 0-3, 4-10, and 11-15 years prior to sampling (August-September 2010), respectively. Natural Wetlands (n = 4) were depressional, Palustrine Emergent. Species were considered invasive if targeted during plant control programs in New York or surrounding states (various sources). Means were compared with One-way Analysis of Variance and significantly different groups marked with different letters.
Figure 14. Significant ($P < 0.05$) linear changes in soil moisture (a), coarse root biomass (b), and marginally significant ($0.05 < P < 0.1$) linear changes in soil bulk density (c) of the top 20 cm of soil across chronosequences consisting of Wetlands Reserve Program (WRP) sites in west-central New York, USA. Soil moisture and bulk density changes refer only to sites restored following non-tillage agriculture ($n = 5$). Coarse root biomass changes refer only to the upland meadow zones of WRP sites restored following tillage and non-tillage agriculture ($n = 17$). Dashed lines are estimated pre-restoration baselines: means of several untilled (a, c) and tilled agricultural fields (b). Recovery times or the number of years following restoration at which belowground parameters will match the mean of four natural reference wetlands (solid black squares with one standard error bars) assume constant linear changes and are based on extrapolated linear regression lines.
Figure 15. Changes in carbon-based soil properties across chronosequences consisting of upland meadow zones of Wetlands Reserve Program (WRP) sites in west-central New York, USA. WRP sites in each chronosequence had been restored from tillage (a-b) or non-tillage agriculture (c) between 0-15 years prior to sampling (October 2010). WRP data points (solid black circles) pertain only to the upland meadow zones of the restoration sites and describe the uppermost 20 cm of soil. Y-axes are in percent change units so that WRP data points show the direction and proportional magnitude of change in the specified soil parameter since being restored from agricultural fields. Dashed black lines represent agricultural (pre-restoration) baselines from which percent changes were calculated (footnotes below provide for interpretations for numbered data points marked as examples). Solid black lines are linear regression lines of marginal significance (0.5 < P < 0.1 at α = 0.05). Regressions lines were extrapolated to calculate recovery times or the number of years following restoration at which soil parameters will match that of the average reference wetland (solid black squares with one standard error bars) assuming constant linear increases.

1. WRP meadow that had been restored for 12 years at the time of sampling and had increased soil organic matter stocks by 130% on a gravimetric basis (g m⁻²) since being restored from a tilled agricultural field.
2. WRP meadow that had been restored for 7 years at the time of sampling and had remained at agricultural levels (0% change) since being restored from a tilled agricultural field.
3. WRP meadow that had been restored for < 1 year at the time of sampling and had experienced a 30% decrease in soil potentially mineralizable carbon since being restored from untilled agricultural field.
4. The mean of four, naturally-occurring reference wetlands (standard errors bars too small to be visible) which indicates that, starting from the agricultural baseline, WRP meadow zones would have to gravimetrically increase their soil potentially mineralizable carbon pools by 315% to match the degree of difference that exists between the peripheral zones of natural wetlands (analogous to WRP meadow zones) and comparable, untilled agricultural fields.
Figure 16. Significant ($P < 0.05$) linear changes in select vegetation parameters (measured August-September 2010) across chronosequences consisting of Wetlands Reserve Program (WRP) sites in west-central New York, USA. Calculations of richness (a) excluded woody plants exceeding 1 m in height and values pertain only to the emergent vegetation zones of WRP sites restored from tillage agriculture ($n = 12$). Forb cover values (b) refer to whole WRP sites restored from tillage and non-tillage agriculture ($n = 17$). Annuals cover data (c) are from the upland meadow zones of WRP sites restored from non-tillage agriculture ($n = 5$). Litter mass data (d) are from the emergent vegetation zones of WRP sites restored from non-tillage agriculture. Recovery times or number of years following restoration at which parameters will match the mean of four natural reference wetlands (solid black squares with one standard error bars) assume constant linear changes and are based on extrapolated, linear regression lines.