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Seeding Density Alters the Assembly of a Restored Plant Community after the Removal of a Dam in Southern Wisconsin, USA

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Abstract: Recently exposed reservoir sediments, prone to colonization by invasive species, provide novel settings to test hypotheses related to soil conditions and propagule supply as potential drivers of plant assembly in disturbed ecosystems. We used a dam removal site in southwestern Wisconsin to examine the relationship between the physiochemical properties of dewatered sediments, seeding density, and plant community assembly. The plant communities from five seed densities (1000, 500, 250, 125, and 0 seed m^{-2}) were annually assessed over four years. We hypothesized (1) that the native aboveground biomass and the proportion of native to invasive (non-seeded species) aboveground biomass would increase with the seeding density and (2) that the diversity of seeded native species would increase with a higher seeding density. We found evidence that sowing at least 500 seeds m^{-2} of prairie species increased their abundance, establishment, and plot diversity compared to non-seeded plants that persisted four years after seeding ($p < 0.05$). The seeding density treatments led to the assembly of two distinct communities: "native" and "invasive". The "native" community, assembled in plots seeded with at least 500 seeds m^{-2}, had a greater aboveground biomass and diversity (i.e., richness) of seeded plants compared to plots with lower seed densities, and its productivity was positively related to this richness. In the "weedy" community, the diversity of invasive species had no relationship to their aboveground biomass, likely because these species share similar traits (i.e., redundancy) and may have performed similar functions within the plant community. These findings suggest that the seeding density interacted with the disturbed soil resources to increase the diversity and productivity of seeded native species and may serve as a positive feedback mechanism for the establishment of native communities in dewatered sediments.

Keywords: dam removal; restoration; seedling density; Wisconsin; invasive species; native species; competition; richness; plant communities; prairie

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1. Introduction

Variations in soil's physiochemical properties and the availability of plant propagules represent proximate controls over net primary productivity and the assembly of plant communities, especially in the restoration of disturbed landscapes. Natural and anthropogenic disturbances often alter soil resource availability and spatial distribution, with a concomitant change in propagule supply [1–3]. In particular, disturbances that remove endemic vegetation from the ecosystem can reduce local competition and increase the availability of resources, leading to the establishment of opportunistic endemic and non-native species [4,5]. Ecological restorations that quantitatively assess the environmental changes caused by disturbances have been shown to minimize these unplanned outcomes [6,7], especially for disturbed ecosystems that are susceptible to colonization by opportunistic species [8,9].

Dam construction and removal exemplify an anthropogenic disturbance that modifies both the abiotic and biotic conditions controlling riparian ecosystems' natural functions. The subsequent proliferation of opportunistic species that frequently occurs after disturbance is often attributed to increases in nutrient availability and the redistribution of soil resources [5,10,11]. During impoundment, the ecosystem's hydrology is altered, riparian vegetation is submerged, and nutrient-rich sediments often accumulate upstream of the dam and within the impoundment [12,13]. Removal of a dam and the subsequent drawdown facilitates the transport and sorting of sediments that help define an abiotic gradient associated with the distribution of soil particles [3,14]. These newly exposed sediments, and the edaphic properties of the dewatered reservoir, can differ significantly, chemically and spatially, from pre-inundation conditions [3,13], which often facilitates the colonization of invasive species [15,16] even after the site being sown with endemic species [17].

Abiotic conditions aside, the recovery of native communities in disturbed systems, especially those prone to invasion by opportunistic species, is often limited by seed recruitment and the viability of the exposed seed bank [18–20]. Moreover, early successional species (native or non-native) are often annual and typically yield persistent and abundant seed banks [21], ready to exploit the variety of environmental conditions when the opportunity for germination presents itself [22]. Conversely, perennial grasses and mid- to late-successional forbs proliferate primarily through vegetative propagation and the production of ephemeral seeds [23–25]. Thus, after disturbances, the probability of native community re-assemblage is disadvantaged, especially if the endemic species and their propagules have disappeared from the surrounding areas during or prior to the disturbance (e.g., [26–29]). Therefore, at first approximation, the re-establishment of these communities may require adding native seeds to outcompete opportunistic invasive species from colonizing these sites [30].

Seeding native species may be insufficient for restoring the endemic plant communities in disturbed areas, when environmental conditions for seedling establishment are hostile to their establishment. Restoring a plant community can only be deemed successful when the sown species germinate and the seedlings survive, establish, and assemble a productive and diverse plant community. However, for some species, seedling emergence is sparse due to a low germination rate, while for others, establishment may be difficult due to competition for resources with opportunistic invasive species and herbivores. Adding diverse seed mixes, sown at a high density, with species of a different successional status may be necessary not only to enhance the native establishment but also to limit the competition of early, more aggressive species [31,32]. Moreover, the added sown species may provide a broader suite of functional services [33].

Recently disturbed ecosystems prone to invasive species provide unique opportunities to test hypotheses related to native dispersal limitations, altered abiotic conditions, and plant interactions as potential controls over the assembly of communities. In addition, these settings also facilitate the a priori design and testing of experiments that incorporate the altered properties of the disturbed system [34,35]. The recent and ongoing removal of dams in the state of Wisconsin (over 174 dams before 2008; Helen Sarakinos, River Alliance of Wisconsin, personal communication) provides such opportunities to study the development of plant assemblages on newly exposed sediments. Previous studies on these sites have shown the edaphic properties of these former impoundments to differ significantly from pre-inundation conditions [3], with newly exposed sediments post-disturbance lacking viable endemic seeds and favoring colonization by well-dispersed opportunistic invasive species such as stinging nettle (*Urtica diocia*) and reed canary grass (*Phalaris arundinacea*) [16,17]. Therefore, the number of seeds is a key factor to consider when restoring reservoir sediments. Although several studies have incorporated seeding densities in ecological restoration (e.g., in [36–38]), to our knowledge, few studies have examined plant community assembly on dewatered sediments; to date, none have coupled this examination with changes in seeding density [16,17], but see [39]. Such research is timely, as the prevalence of these sites is predicted to increase nationwide, with most dams

aging past their 50-year life expectancy [40]. Moreover, throughout Wisconsin, examples of *Phalaris arundinacea* proliferation are abundant [41,42].

The objectives of this study were to identify the effects of seeding density and soil physiochemical properties on the restoration of the plant community following the removal of a dam in southern Wisconsin within a dewatered reservoir that lacked viable endemic seeds [16]. This field-based experiment used a replication of four seeding densities of mesic prairie species and a control treatment without seed application to investigate their interaction with soil properties and surrounding self-colonizing species. We hypothesized that sowing seeds of native species at a high density would produce plant communities more abundant (greater aboveground biomass) in native species and diversity compared to non-seeded species. We predicted that (1.) the percentage of the seeded species' aboveground biomass would increase with the number of seeds added (i.e., seeding density) relative to non-seeded species, that (2.) there would be a greater diversity of the seeded native species in the plots sown at a higher seeding density, and that (3.) these differences would occur regardless of spatial differences in the soil's physiochemical properties. We also predicted that the composition of the plant community assembled under higher-seeding density treatments would differ from the plant community assembled in the control plots. Finally, we quantified the relationship between physiochemical soil properties, seed density, and plant community within the former impoundment to help explain our results.

2. Materials and Methods

The four-year (2005–2009) study was conducted within the reservoir sediments of the former Beers Dam located at Franbrook Farm, a University of Wisconsin–Madison research station in the unglaciated region of southern Wisconsin (42°44′ N, −89°45′ W) (Figure 1). The soil climatic regime is mesic and udic, with a mean annual air temperature of 8.8 °C and mean annual precipitation of approximately 964 mm (100 mm is snow); approximately two-thirds of the precipitation falls during the growing season, from April to October. During the five years of the study (2005–2009), the mean air temperatures were 9.2 °C, 9.6 °C, 8.4 °C, 7.5 °C, and 8.2 °C, respectively. Annual precipitation for these years was 650, 1017, 1086, 1206, and 1155 mm, respectively (http://www.usclimatedata.com/climate/monroe/wisconsin/united-states/uswi1232, accessed 14 August 2006). The soils within the study area were formed from loess deposits (Peorian Age) over dolomite and sandstone and originally mapped as a Chaseburg silt loam (coarse silty, mixed, superactive, nonacid, mesic Typic Udifluvents), with the northwestern corner characterized as a Northfield loam (loamy, mixed, active, mesic Lithic Hapludalfs) [43]. The sediment deposits during inundation (described below and previously in [3]) were lacustrine and alluvial in origin. The historic plant communities of the area consisted of tallgrass prairie and oak savanna, with grasses and sedges dominating the riverbank and upland floodplains [44,45].

2.1. Soils Properties and Seed Bank

In 2003, the Wisconsin Department of Natural Resources removed the 43-year-old dam and sowed the reservoir sediments with annual rye grass (*Lolium multiflorum*) to provide cover and stabilize the newly exposed sediments. The stream that dissected the former impoundment was allowed to adjust naturally after dam removal. In 2005, we determined that the impoundment homogenized the deposited sediments, that these sediments differed in physiochemical properties compared to the soils they buried, and that the subsequent dam removal defined an abiotic gradient associated with the transport of finer sediments downstream during the dewatering process (Table 1; [3]).

A preliminary study of the sediment seed bank (0–0.15 m in depth) from the impoundment showed a lack of endemic seed species (data are not presented here). Not surprisingly, the most prevalent species found was *Lolium multiflorum* (1860 seeds m^{-2}). In addition, we found seeds of two annual, early successional species, *Chenopodium album* (600 seeds m^{-2}) and *Stellaria media* (47 seeds m^{-2}), plus seeds of unidentified species (143 seeds m^{-2}).

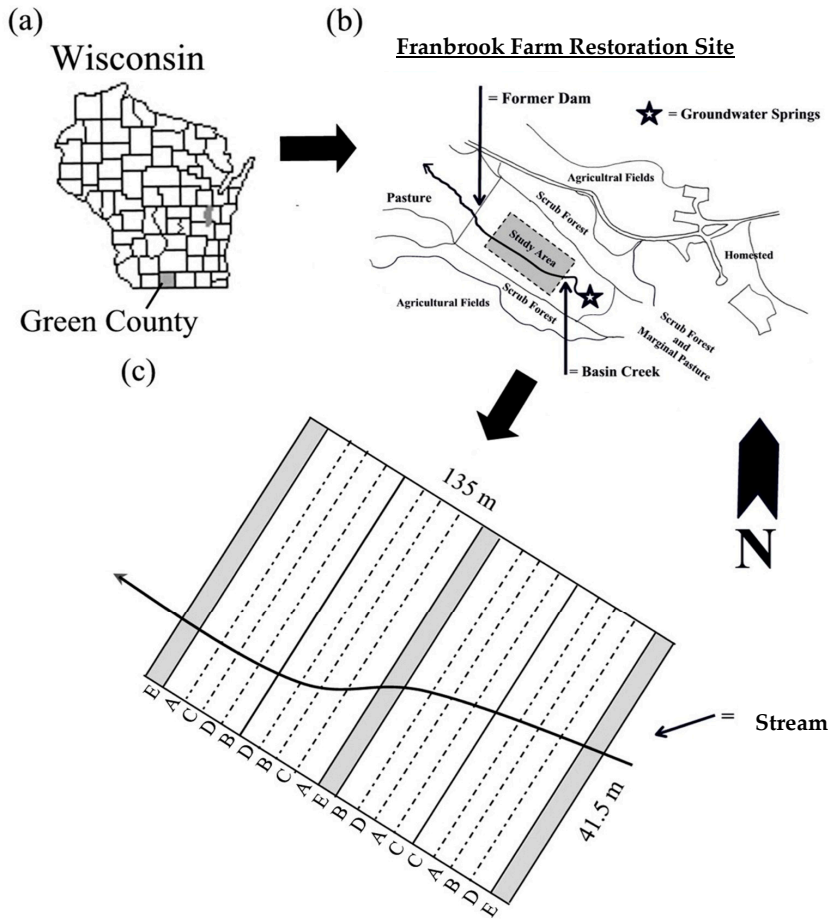


Figure 1. Study site map of a drained reservoir in Green County, Wisconsin (**a**). The research site was located in the approximate center of the dewatered basin, where the stream naturally flows (**b**). The 133 by 41.5 m research area was divided into four blocks along the stream, and randomly assigned within each block was one of four (7 by 41.5 m) treatments plots. The treatments represented seeding mixes at four densities (A = 1000, B = 500, C = 250, and D = 125 seed m^{-2}). Three control plots (E = control) without a seed application were placed at the beginning, middle, and end of the area (**c**). Maps are not drawn to scale.

In the spring of 2005, we delineated a 133 m by 41.5 m rectangular area in the approximate center of the former reservoir dissected by a spring-fed stream that flowed down the longitudinal center of the basin (Figure 1b,c). Based on the assumed and later measured physiochemical gradient that the disturbances (dam construction and dam removal) created [3], we divided the area along this gradient into four blocks and randomly assigned four seeding density treatments (7 m by 41.5 m plots) within each block. The treatments consisted of seed mixes at four densities (A = 1000, B = 500, C = 250, and D = 125 seed m^{-2}; John Harrington, personal communication). We also established three plots without a seed application at both ends and in the middle of the study area (E = control; Figure 1c) to serve as internal controls. The seed mixes included 12 grasses (40% of seeds per mix) and 30 native forbs (60% of seeds per mix) of a different successional status and consistent with the endemic mesic prairies in southwestern Wisconsin ([45]; Table 2). We broadcast the mixes by hand, allowing them to grow and compete naturally. We seeded a buffer area around the research site with a less diverse mix of native plants to help standardize the initial native-to-invasive seed bank surrounding the research plots.

Table 1. Mean physiochemical properties from the surface 0.15 m of the reservoir sediments, and linear regressions between the physiochemical properties of reservoir sediments and the longitudinal distance, west to east, from the former Beers Dam at Franbrook Farm, Green County, Wisconsin in 2004. To avoid scientific notations, the soil physiochemical properties are presented in g m^{-2} where necessary. Data reproduced from [3].

Property	Mean	SD	CV	r^2	*p*-Value
Soil physical properties [a]					
Bulk density (g cm^{-3})	1.01	0.01	0.10	0.81	<0.001
Sand, (%)	2.83	1.94	0.68	0.57	<0.001
Silt, (%)	79.30	7.04	0.09	0.51	<0.001
Clay, (%)	17.87	7.59	0.42	0.74	<0.001
Soil chemical properties					
pH	7.93	0.11	0.01	0.35	=0.060
Total soil carbon (kg m^{-2})	5.22	0.62	0.12	---	---
Total soil nitrogen (kg m^{-2})	0.31	0.04	0.12	0.27	<0.010
NH_4-N (g m^{-2})	1.73	0.18	0.10	---	---
NO_3-N (g m^{-2})	4.13	1.67	0.40	0.26	<0.010
Soil phosphorus (kg m^{-2})	0.09	0.01	0.11	0.56	<0.010
Bray P (g m^{-2})	0.58	0.27	0.46	0.57	<0.001
Soil potassium (kg m^{-2})	0.46	0.04	0.08	---	---
Bray K (g m^{-2})	12.61	3.08	0.24	---	---
Calcium (kg m^{-2})	6.97	1.22	0.18	---	---

Sediments refer to soil deposits following dam construction. [a] Abbreviations in Table 1 (above): Bray P = extractable phosphorus, Bray K = extractable potassium.

2.2. Plant Community Measurements

We surveyed the restored plant community at peak aboveground biomass production in the former reservoir each year from 2006 to 2009. To estimate mean changes in the restored vegetation, we divided each of the nineteen plots into five 7 m by 7 m subplots. Within each plot, we excluded a 6.5 m buffer where the stream separated the south side of the plot from the north (Figure 1c). In each subplot, we randomly placed a 0.50 m by 0.50 m quadrat on the ground to identify and record all the species within each quadrat, harvest all the aboveground biomass (as an estimate of the net annual aboveground primary production), and then separate all the harvested plants by species. When necessary, individual plants were pressed and later identified using the appropriate keys [46] on the Robert W. Freckmann Herbarium Plants of Wisconsin Database (https://wisflora.herbarium.wisc.edu/index.php, accessed 2 October 2007). At the lab, all the aboveground biomass was air-dried in a forced air oven at 65 °C to a constant mass for 48 h and then weighed to the nearest 0.01 g. We sorted and quantified the aboveground biomass (g) by species per plot and then pooled the totals into two vegetation categories. One category included the native seeded plant species, while the other category included any of the plant species that emerged (whether native or non-native opportunistic species) and were not included in the seed mix. Henceforth, all seeded native plants will be referred to as *seeded* species, and any species not included in the seed mix will be referred to as *non-seeded* species. We calculated the mean aboveground biomass of the pooled seeded species, of the pooled non-seeded species, and of the complete set of species, and finally calculated the percentage aboveground biomass of the seeded species (%, g g^{-1}), to normalize multiple comparisons across the treatments.

Table 2. Grass and forb mesic prairie species and respective percentages of seeds included in planting mixture †.

	Scientific Name	Common Name	Percent of Seed Mix
Grasses			40.0
	Andropogon gerardii	Big bluestem	5.0
	Bromus kalmii	Prairie brome	10.0
	Calamagrostis canadensis	Canada blue joint	5.0
	Carex bicknelli	Bicknell's sedge	5.0
	Carex vulpinoidea	Fox sedge	15.0
	Elymus canadensis	Canada wild rye	15.0
	Elymus villosus	Silky wild rye	10.0
	Panicum virgatum	Switchgrass	5.0
	Schizachyium scoparium	Little bluestem	10.0
	Spartina pectinata	Prairie cord grass	5.0
	Sporobolus heterolepsis	Prairie dropseed	10.0
	Sorghastrum nutans	Indian grass	5.0
Forbs			60.0
	Allium cernuum	Nodding wild onion	3.0
	Amorpha canescens	Lead plant	3.5
	Asclepias incarnata	Swamp milkweed	3.0
	Asclepias tuberosa	Butterfly milkweed	3.5
	Aster laevis	Smooth blue aster	3.5
	Aster novae-angliae	New England aster	3.0
	Baptisia leucantha	Wild white indigo	1.5
	Cacalia suaveolens	Sweet Indian plantain	2.0
	Coreopsis palmata	Prairie coreopsis	4.0
	Desmodium canadense	Canada tick-trefoil	3.5
	Dodecatheon meadii	Shooting star	1.5
	Eryngium yuccifolium	Rattlesnake master	3.5
	Eupatorium perfoliatum	Boneset	3.5
	Gentiana andrewsii	Bottle gentian	2.0
	Heliopsis helianthoides	Early sunflower	5.5
	Heuchera richardsonii	Alumroot	2.0
	Lespedeza capitata	Round-headed bushclover	3.5
	Liatris aspera	Rough blazing star	5.0
	Liatris pycnostachya	Prairie blazing star	2.0
	Monarda fistulosa	Wild bergamot	5.5
	Petalostemum purpurea	Purple prairie clover	3.5
	Ratibida pinnata	Yellow coneflower	2.0
	Rudbeckia subtomentosa	Sweet black-eyed Susan	5.5
	Silphium laciniatum	Compass plant	3.5
	Silphium terebinthinaceum	Prairie dock	1.5
	Solidago rigida	Stiff goldenrod	5.5
	Tradescantia ohiensis	Spiderwort	5.5
	Verbena hastata	Blue vervain	2.0
	Veronicastrum virginicum	Culver's root	1.0
	Zizia aurea	Golden Alexander	5.5

† The seed mixtures included 12 species of native grasses (40% of the total number of seeds per mix) and 30 species of native forbs (60% of the total of number of seeds per mix). Each seed mix was designed such that aggressive species were in limited numbers, to allow other less aggressive species to grow; therefore, the proportion of each species varied.

2.3. Community Composition and Structure

To compare the effect of seeding density on the composition of the plant community that assembled in the reservoir sediments, we measured and compared the (α) diversity of the communities (the seeded, non-seeded, and whole community) within each seeding treatment each year and compared the annual changes (turnover β diversity) in these

communities [47]. We used aboveground biomass, instead of plant density or cover, as an estimate of species abundance, because the production of biomass best reflects differences in resource utilization among plants in competitive settings [48] and provides the least subjective measure. We estimated the relative abundance for each species and then species richness, diversity, and evenness per treatment (i.e., seeding density) for each of the four years of this study. We determined richness, S, as the number of species per treatment, and diversity with the Shannon–Wiener H' index:

This is example 1 of an equation:

$$H' = -\Sigma p_i \ln (p_i) \quad (1)$$

where p_i represents the proportion of the total biomass by each species i, and the evenness, E, is

$$E = H'/\ln S \quad (2)$$

The annual species turnover, or β diversity, was determined with Whittaker's statistic:

$$\beta_W = (S/S_r) - 1 \quad (3)$$

where S is the number of species in the two communities in time (i.e., over the four years of the study) and space, and S_r is the mean species richness of each community [49].

2.4. Soil Properties

In 2009, the last year of the study, we quantified the physiochemical properties of the reservoir sediments assumed to comprise the majority of root proliferation. We collected a set of three sediment samples at a depth of 0–0.15 m for each plot. The samples were transported to the lab, composited per plot, air-dried, passed through a 2 mm sieve, and analyzed for cations at the University of Wisconsin Soil and Plant Analysis Laboratory. The volumetric soil moisture content was measured in the sediments approximately every two weeks during the growing season at two random sampling points in each plot, one at the north and the other at the south side of the plot. Soil moisture content was measured with a Dynamax© TH_2O probe (Houston, TX, USA) at a depth of 0–0.15 m.

2.5. Statistical Analysis

We performed a repeated measures analysis of variance to determine the effect of seeding density and the time after seeding on plant community variables (i.e., the aboveground biomass of the seeded species, aboveground biomass of the non-seeded species, total aboveground biomass, percentage aboveground biomass of the seeded species, and diversity indices). The statistical models were tested using mixed models. We calculated a type III F test for the fixed effects of seeding density and year, and their interaction. The random effects included the block and the interaction between the block and seeding density. We used the Tukey–Kramer ($\alpha < 0.05$) "honestly significant difference" (HSD) to make pairwise comparisons of the least squares means between effect variables (seeding density and year) and their interaction. All variables were tested for normality and equal variance using Shapiro–Wilk's statistic and transformed when necessary.

We quantified the relationship between aboveground biomass and plant diversity (richness) for each type of vegetation (i.e., seeded and non-seeded species) by fitting a regression line for each vegetation type. The regressions were performed with the aboveground biomass and species richness, using data from the four years of the study. We compared the slopes of the two regression lines to assess the effect of each vegetation type on the relation between diversity and aboveground biomass productivity. The regression models were tested using mixed models, with vegetation type and richness (the continuous variable) as fixed effects and the block as a random effect. The variables were tested for normality and equal variance using Shapiro–Wilk's statistic and transformed when necessary. We understand that using aboveground biomass as an index of ecosystem productivity

may be less informative than using net primary productivity (NPP), particularly where above- and belowground allocation patterns differ across species, since NPP incorporates both belowground and aboveground biomass [50]; however, aboveground biomass is a widely used index of ecosystem functioning, to estimate the aboveground component of plant productivity [51–54].

Differences in species composition among the seeding treatments were assessed using principal component analysis (PCA) for each year separately. The PCA was performed on the abundance (i.e., aboveground biomass) of each species in all of the treatment plots, as it reduces the dimensionality of multivariate data and transforms a set of variables (e.g., species abundance) into a set of uncorrelated variables called principal components [55]. The abundance data were standardized to meet normality requirements. The principal component scores were treated as dependent variables, and an analysis of variance was used to test for differences among the seeding treatments in plant composition each year. Orthogonal contrasts were then employed to estimate the seeding density effect on plant community composition. Ordination biplots were generated from the mean principal component scores for each seeding treatment for each year, to visualize the treatment effects on species composition.

We further analyzed the effect of edaphic site variables and seeding density on the assembly of the plant community (seeded and non-seeded species), using a canonical correspondence analysis (CCA). We chose the first growing season after seeding (2006) and the last year of the study (2009), because we assumed they would best capture temporal changes due to succession. CCA is a multivariate statistical technique that identifies patterns of variation in species composition explained by their environment [56]. It combines ordination and regression techniques to yield ordinations in species data (e.g., abundance) that are constrained by their relationships to environmental variables. For the analysis of the first year growing season, we used seeding density and the soil properties that we previously measured before we sowed the reservoir sediments [3]. The species data for this analysis consisted of the species abundance (i.e., aboveground biomass) in 2006, one year after seeding. A similar analysis was performed for the last year of the study (2009), using seeding density and the soil variables and species abundance measured that year. We selected predictor environmental variables for the analysis based on correlations between the soil variables, so that uncorrelated soil variables were selected. We performed a CCA for all the species in the research plot, optimized the species scores ($\alpha = 0$), and tested the statistical significance of the canonical axes with Monte Carlo permutations. The species data were double-relativized, and environmental variables were transformed when necessary. Both ordination analyses assume species abundance can be described as a linear function of the position along the environmental gradient that the dewatering defined.

All the analyses of variance and regression were performed with SAS v9.2 (SAS Institute, Inc., Cary, NC, USA), and the diversity indices were determined with the package vegan (https://cran.r-project.org/web/packages/vegan/index.html, accessed 24 December 2010) in the R programming environment [57]. Finally, the two ordination analyses were performed with PC-ORD (V.5; MjM Software Design, Gleneden Beach, OR, USA).

3. Results

3.1. Aboveground Biomass

Over the four years of this study, higher seeding densities yielded significantly greater aboveground biomass for the seeded species ($F_{4,11} = 16.85$, $p < 0.001$). For example, on average, adding 1000 seeds m^{-2} produced a greater aboveground biomass (338 ± 70.4 g m^{-2}) for seeded species, relative to plots receiving 125 seeds m^{-2} or less (Figure 2). Although seeding density only had a marginally significant effect ($F_{4,11} = 2.98$, $p = 0.07$) on the average aboveground biomass of the non-seeded species, we observed a decreasing trend from 392 ± 81.2 g m^{-2} in plots with no seeds applied to 293 ± 70.3 g m^{-2} in plots sown with 1000 seeds m^{-2}.

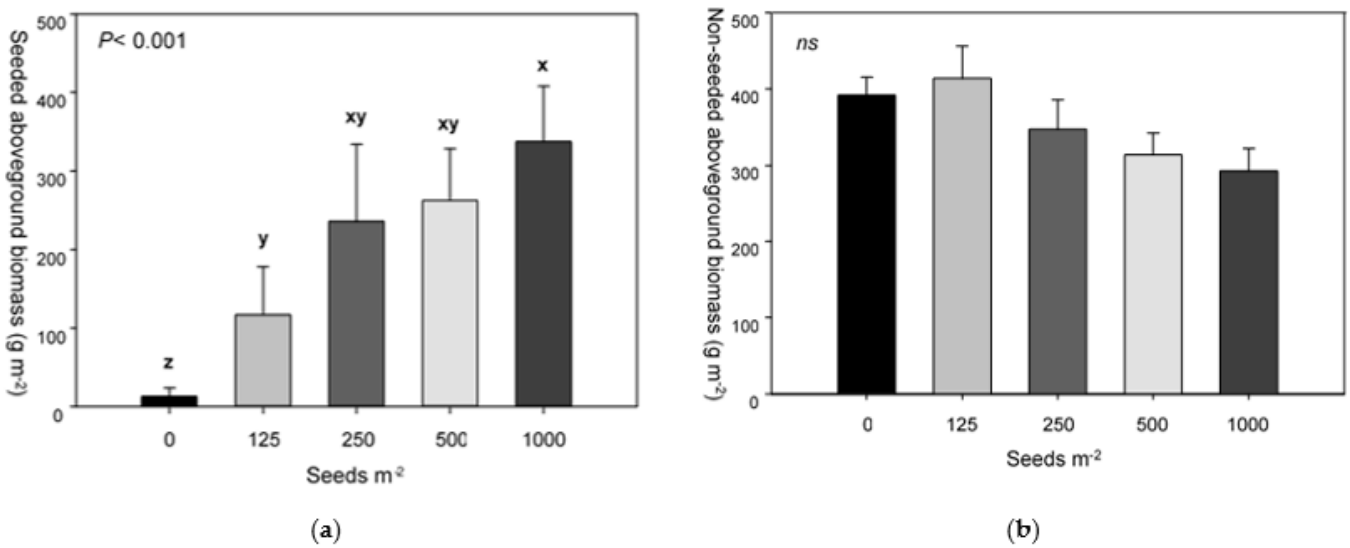


Figure 2. Differences in mean (**a**) seeded species and (**b**) non-seeded aboveground biomass (g m^{-2}) among seeding density treatments. Standard errors are plotted with aboveground biomass means over four years (2006–2009) after seeding; there was no significant interaction between year and treatment. Different letters denote significant differences among seeding density treatments at $p < 0.05$.

Regardless of seeding density, the aboveground biomass of seeded species increased significantly ($F_{3,42}$ = 23.90, $p < 0.001$) after three years of sowing the sediments, while the non-seeded species significantly decreased ($F_{3,42}$ = 7.18, $p < 0.001$) after two years (Figure 3). On average, seeded species' aboveground biomass increased from 14 ± 5.0 to 341 ± 65.9 g m^{-2}, in contrast to the non-seeded species, which decreased from a mean of 459 ± 23.4 g m^{-2} to 306 ± 37.8 g m^{-2} from 2006 to 2009, respectively. Consequently, the mean aboveground biomass of the entire community (seeded plus non-seeded species) changed annually ($F_{3,42}$ = 9.55, $p < 0.001$) from 473 ± 24.5 g m^{-2} in 2006 to 393 ± 26.6 g m^{-2} in 2007 and then increased to 647 ± 59.1 g m^{-2} in 2009.

When examining the percentage of aboveground biomass of seeded species within the entire community (%, g g^{-1}), we found a significant interaction between time after seeding and seeding density, most notably in 2009 ($F_{12,42}$ = 2.58, p = 0.012; Figure 4). In 2009, higher seeding densities (≥500 seeds m^{-2}) led to a greater percentage of seeded species aboveground biomass (>60%) compared to the lower seeding densities (<125 seeds m^{-2}). Moreover, the mean aboveground biomass of the entire community increased from 2006 to 2008; however, in 2009, all plots produced the same percentage of seeded species aboveground biomass as the previous year, except for the 500 seeds m^{-2} treatment, which increased from 48% in 2008 to 69% in 2009 (Figure 4).

3.2. Community Composition

Initially, all the plots were strongly dominated by early successional fast-growing species, but these were replaced with perennial species by 2009. The three most dominant species (*Lactuca serriola*, 42%; *Lolium multiflorum*, 27%; and *Stellaria media*, 9%) decreased from 78% of the total aboveground biomass in 2006 to slightly over 3% in 2009. Two of these species were non-seeded plants, while the other was the cover crop graminoid sown after dam removal (*L. multiflorum*). By 2009, four perennial species replaced the dominance of early successional plants; the four most abundant plants produced approximately 67% of the total aboveground biomass. Two were the seeded forbs *Heliopsis helianthoides* (22%; 2661 g m^{-2}) and *Monarda fistulosa* (17%; 2020 g m^{-2}), and the other two were non-seeded species: *Phalaris arundinacea* (16%; 2010 g m^{-2}) and *Solidago canadensis* (13%; 1543 g m^{-2}). The cover crop *Lolium multiflorum* had no effect on the abundance of the seeded species

across the seeding density treatments. After five years, the relative abundance of the cover crop was only 2% of the plant community, although there was a slightly higher abundance (4–5%) of this species in plots with the lower seeding density treatment (125 seeds m^{-2}) and in the control plots.

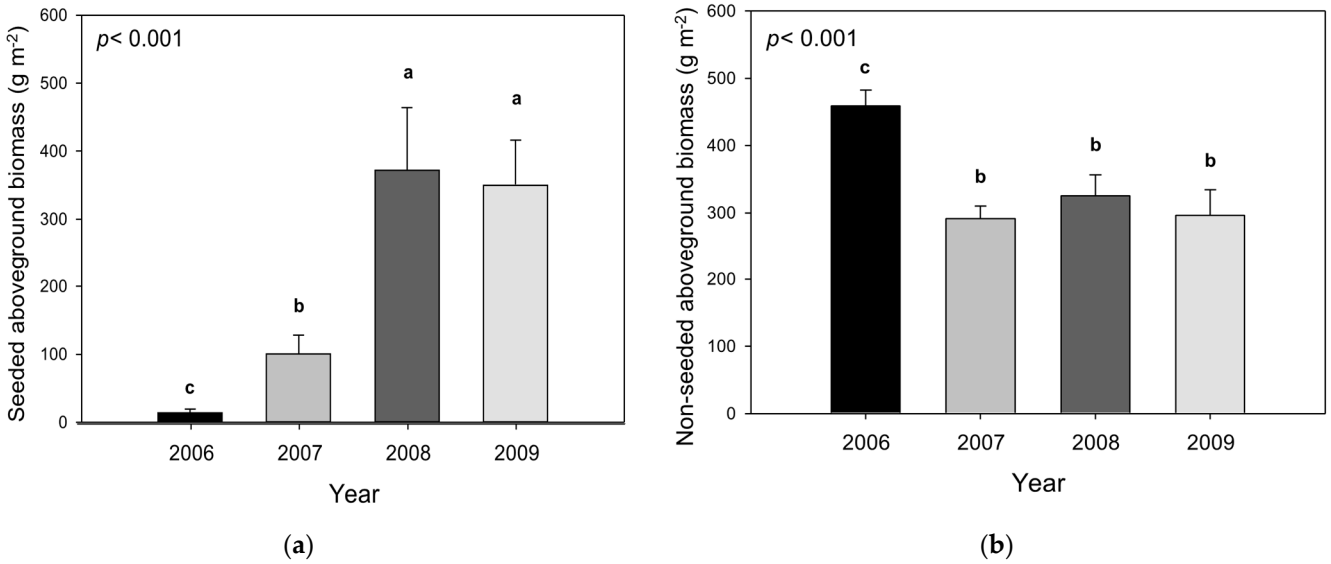


Figure 3. Differences in mean (**a**) seeded and (**b**) non-seeded aboveground biomass (g m^{-2}) among four years of seeding. Standard errors are plotted with annual aboveground biomass means independent of seeding density; there was no significant interaction between year and treatment. Different letters denote significant differences among the years after seeding at $p < 0.05$.

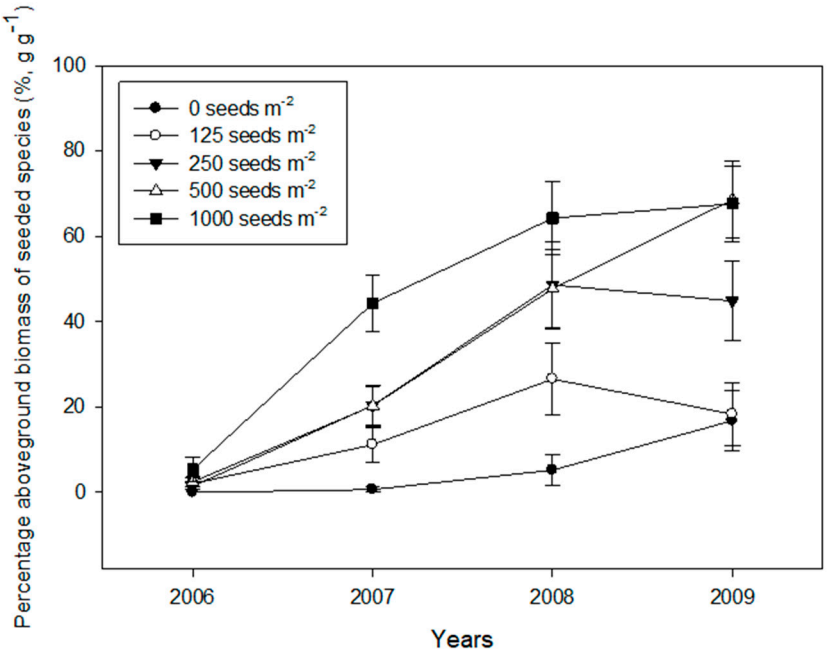


Figure 4. Annual differences in the percentage of the seeded species aboveground biomass (%, seeded species g g^{-1}) among the different seeding densities. Standard errors are plotted around the aboveground biomass means.

Despite visual separation of the treatments in the annual PCA biplots, the analysis of variance only revealed significant differences within the first principal component (PC1)

scores in 2007 ($F_{4,11}$ = 4.87, $p < 0.05$) and 2009 ($F_{4,11}$ = 4.45, $p < 0.05$) (Figure 5). In 2006 and 2008, the seeding density assemblage plots were statistically similar, while in 2007 and 2009, the higher-seeding assemblage plots diverged into two distinct trajectories. In 2007, the scores of the PC1 explained 17% of the variability in aboveground biomass of the plant communities relative to seeding density (Figure 5b). Moreover, the orthogonal contrasts following the analysis of variance demonstrated that the highest-density treatment (1000 seeds m^{-2}) corresponded to a plant community dominated by seeded species (positive loadings), which differed from the communities formed under the other treatments in that year (Table 3). Two years later, in 2009, the scores of the PC1 explained 11% of the variation among treatments, again defining different plant communities. In this year, the treatments separated into two distinct groups along PC1, where seeded species (negative loadings) dominated community assemblages under the two higher-seeding density treatments (at least 500 seeds m^{-2}), while invasive species (positive loadings) dominated in plots sown with less than 250 seeds m^{-2} (Figure 5d).

3.3. Diversity of Plant Communities

The results from the annual plant surveys showed that the total number of species that emerged in the reservoir sediments increased by 33%, from 33 species (9 seeded and 24 non-seeded) in 2006 to 44 species (13 seeded and 31 non-seeded) in 2009. Indeed, the seeded community became dominated by a small subset of the mixture of 40 native prairie species. Although the number of non-seeded species outnumbered the seeded species during the study, the number of seeded species increased by 44% (9 to 13) over the four years of this study, while non-seeded species increased by only 29%. The species turnover rate or β-diversity (change of number of species per year) was slightly higher in the seeded species (0.33, 0.30, and 0.29 sp sp^{-1} yr^{-1}) than in the non-seeded species (0.27, 0.25, and 0.23 sp sp^{-1} yr^{-1}) for the years 2007, 2008, and 2009, respectively.

Both the seeding density and time after seeding significantly affected the diversity indices of the seeded plant community, without interaction between the variables. The H' index significantly increased with the seeding density ($F_{4,11}$ = 14.71, $p < 0.001$), with the highest mean index of 1.15 ± 0.09 m^{-2} found in the highest-density treatment (1000 seeds m^{-2}), compared to a mean index of 0.19 ± 0.08 found in the control plots (Figure 6a). The mean richness was also significantly greater ($F_{4,11}$ = 23.07, $p < 0.001$) under the highest seeding density treatment compared to the control; for every seeded species in the control plots, there were on average seven seeded plants in the highest-density treatment (Figure 6b). Likewise, evenness was significantly greater for the higher seeding densities, yielding an evenness index of 0.63 ± 0.05 for these plant communities ($F_{4,11}$ = 6.81, $p < 0.01$) compared to the control plots (0.18 ± 0.09). Independent of density, the time after seeding also had a significant effect on the diversity of this plant community, reaching a peak in year 2007 (Figure 7). The H' index value of this community relative to time only increased in 2007 ($F_{3,42}$ = 6.47, $p < 0.01$) from 0.43 ± 0.11 to 0.91 ± 0.12, reaching a plateau thereafter (Figure 7a). Similarly, richness reached a peak (six species per plot) in 2007; however, it decreased afterward to four species per plot through 2009 ($F_{3,42}$ = 13.58, $p < 0.001$; Figure 7b). Consequently, evenness increased significantly with time ($F_{3,42}$ = 5.43, $p < 0.01$), reaching its peak in 2009, the last year of the study.

Neither treatment nor time significantly affected diversity (H' index) in this community (Figure 8a,b). Species richness, however, depended on a significant interaction between treatment and time after seeding ($F_{12,42}$ = 2.35, $p < 0.05$), making it difficult to interpret the main effects (Figure 9). The greatest number of non-seeded species (15 ± 0.9) occurred in 2007 within the highest-density treatment. The least number of non-seeded species (5 ± 0.8) occurred in 2008, also in the highest-density treatment. The mean evenness (0.57 ± 0.02) for the non-seeded plant community was significantly similar, relative to seeding density treatments and time after seeding.

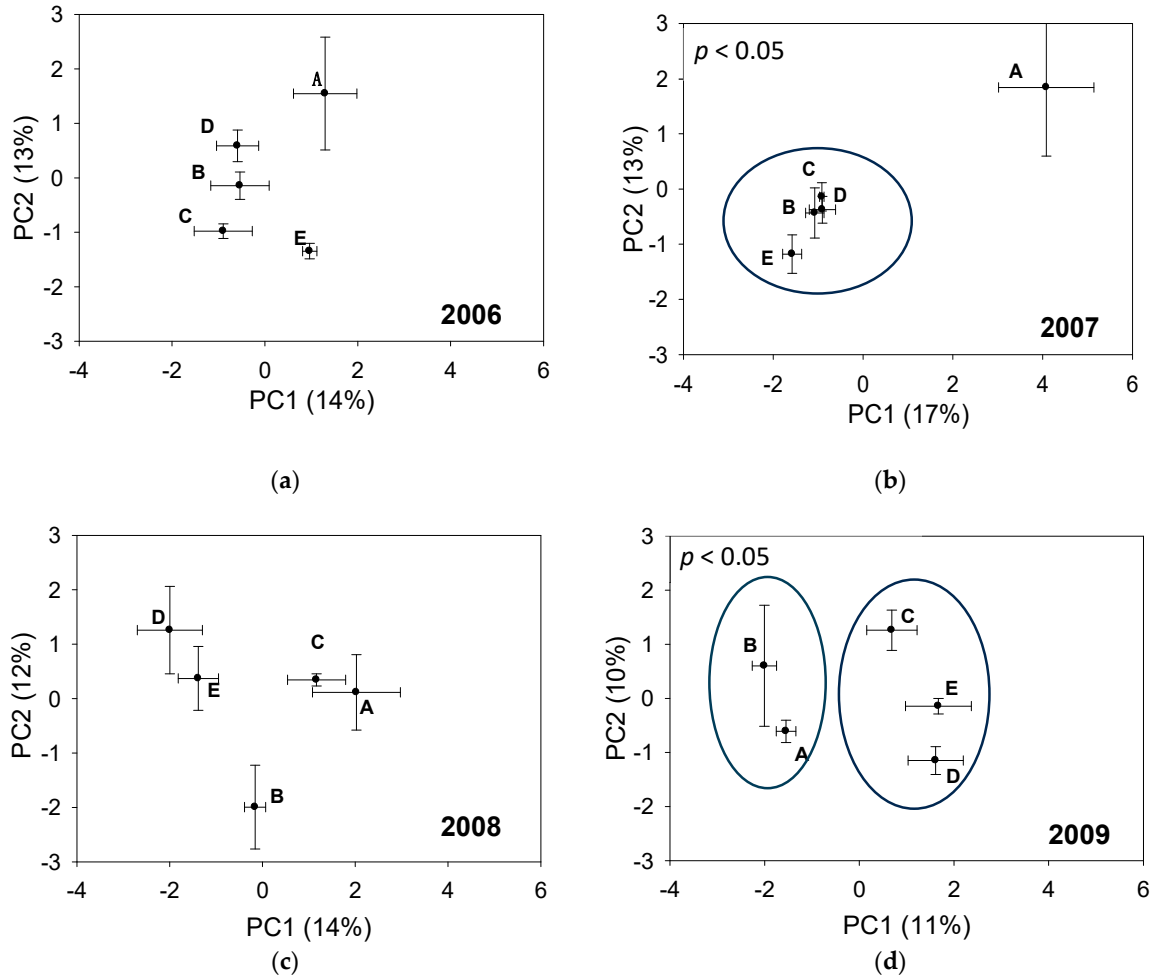


Figure 5. Annual biplots of the two first principal component scores from the PCA of the aboveground biomass of all the species surveyed in this study. Each point represents the mean score of each of the different seeding density treatments (A = 1000, B = 500, C = 250, D = 125, and E = 0 seeds m^{-2}, respectively). Standard errors are plotted around the means. Orthogonal contrast analyses of the PC1 scores revealed significant differences at $p < 0.05$, denoted by circles, among plant communities assembled under the different seeding treatments in the years 2007 (**b**) and 2009 (**d**); no significant differences were found in years 2006 (**a**) or 2008 (**c**).

When comparing species richness to the average aboveground biomass, we found a positive linear relationship over the entire four years of this study for seeded species only; no such relationship was found for the community of non-seeded species (Figure 10). The linear regression of ln–seeded species biomass against ln–seeded species richness was likewise significant ($F_{1,74} = 106.3$, $p < 0.01$). The best-fitting equation regression was ln (seeded aboveground biomass) = 0.47 + 2.86 ln (seeded richness); $r^2 = 0.58$ ($p < 0.01$). No relationship existed between the number of non-seeded species and their aboveground biomass ($r^2 = -0.01$ $p = 0.95$).

3.4. Soil Physiochemical Properties and Seeding Density Effects on Plant Composition

In 2006, the canonical correspondence analysis revealed that the total variance of the species community was 4.9% (Figure 11). Together, all the axes accounted for only 27.6% of the variance. The first axis (CCA1) explained 8.9% of the variance in the plant community, where soil pH had the greatest effect (correlated by 90%) on CCA1. Conversely, axis two (CCA2) explained 8.8% of the total variance of the plant community in 2006, where soil NO_3^-N was highly correlated (95%) with CCA2. Seeding density and soil bulk

density were moderately correlated with CCA2, but opposite to each other, 41% and 49%, respectively. All four vectors were of moderate length, but soil NO_3-N and pH were by far the longest, suggesting these two variables best explained the overall composition of the plant community. From all the soil resources, NO_3-N was strongly associated with the aboveground biomass of the annual *Stellaria media*.

Table 3. The first eigenvectors from the principal component analyses of the aboveground biomass of species present in the years 2007 and 2009.

2007			2009		
Species	**Type**	**Eigenvector 1**	**Species**	**Type**	**Eigenvector 1**
Chenopodium album	I [a]	−0.1089 [b]	*Heliopsis helianthoides*	N	−0.2114
Conyza canadensis	I	−0.0958	*Rudbeckia subtomentosa*	N	−0.2070
Polygonum persicaria	I	−0.0940	*Monarda fistulosa*	N	−0.1803
Oxalis corniculata	I	−0.0934	*Asclepias incarnata*	N	−0.1632
Taraxacum officinale	I	−0.0869	*Carex vulpinoidea*	N	−0.1622
Cirsium arvense	I	−0.0742	*Zizia aurea*	N	−0.1619
Stellaria media	I	−0.0699	*Polygonum persicaria*	I	−0.1467
Hackelia virginiana	I	−0.0686	*Elymus canadensis*	N	−0.1358
Lactuca serriola	I	−0.0667	*Eupatorium perfoliatum*	N	−0.1318
Andropogon gerardii	N	−0.0658	*Ambrosia trifida*	I	−0.1159
Phalaris arundinacea	I	−0.0647	*Digitaria* spp.	I	−0.1067
Aster spp.	I	−0.0600	*Solidago canadensis*	I	−0.1060
Urtica dioica	I	−0.0506	*Arctium* spp.	I	−0.0765
Solidago canadensis	I	−0.0441	*Desmodium canadense*	N	−0.0741
Arctium spp.	I	−0.0363	*Impatiens capensis*	I	−0.0599
Panicum spp.	I	−0.0341	*Panicum* spp.	I	−0.0594
Solidago rigida	N	−0.0311	*Polygonum coccineum*	I	−0.0573
Schizachyium scoparium	N	−0.0297	*Urtica dioica*	I	−0.0548
Chenopodium sp.	I	−0.0272	*Sonchus oleraceus*	I	−0.0544
Lolium multiflorum	I	−0.0164	*Tradescantia ohiensis*	N	−0.0536
Polygonum arenastrum	I	−0.0157	*Phalaris arundinacea*	I	−0.0493
Oenothera biennis	N	−0.0083	*Lolium multiflorum*	I	−0.0489
Trifolium pratense	I	0.0294	*Stellaria media*	I	−0.0355
Erigeron annuus	I	0.0346	*Alliaria petiolata*	I	−0.0258
Cirsium spp.	I	0.0377	*Potentilla simplex*	I	−0.0103
Asclepias incarnata	N	0.0541	*Medicago lupulina*	I	−0.0082
Desmodium canadense	N	0.0591	*Ratibida pinnata*	N	−0.0061
Rudbeckia subtomentosa	N	0.0830	*Ambrosia* spp.	I	0.0302
Asclepias tuberosa	N	0.0888	*Aster* spp.	I	0.0705
Aster novae-angliae	N	0.0918	*Taraxacum officinale*	I	0.0919
Melilotus alba	I	0.0922	*Lactuca serriola*	I	0.1583
Epilobium coloratum	I	0.0973	*Epilobium coloratum*	I	0.1654
Setaria spp.	I	0.1142	*Medicago sativa*	I	0.1713
Elymus canadensis	N	0.1258	*Verbena hastata*	N	0.1713
Heliopsis helianthoides	N	0.1556	*Chenopodium album*	I	0.1778
Monarda fistulosa	N	0.1733	*Chenopodium* spp.	I	0.1832
Ratibida pinnata	N	0.1848	*Erigeron annuus*	I	0.2043
Geum canadensis	I	0.2222	*Cirsium* spp.	I	0.2081
Amaranthus retroflexus L.	I	0.2417	*Geum canadensis*	I	0.2113
Bromus spp.	I	0.2590	*Rosa multiflora*	I	0.2114
Petalostemum purpurea	N	0.2624	*Hackelia virginiana*	I	0.2121
Potentilla simplex	I	0.2974	*Cirsium arvense*	I	0.2830
Digitaria spp.	I	0.3008	*Conyza canadensis*	I	0.2896
Eupatorium perfoliatum	N	0.3064	*Aster novae-angliae*	N	0.3097
Silphium laciniatum	N	0.3254			
Zizia aurea	N	0.3482			

[a] I indicates a non-seeded species; N indicates a seeded species. [b] Each element in the vector is the coefficient (loading) that is multiplied by the value of the corresponding standardized species aboveground biomass. The sum of the products of the standardized biomass and the loadings is the score of the first principal component.

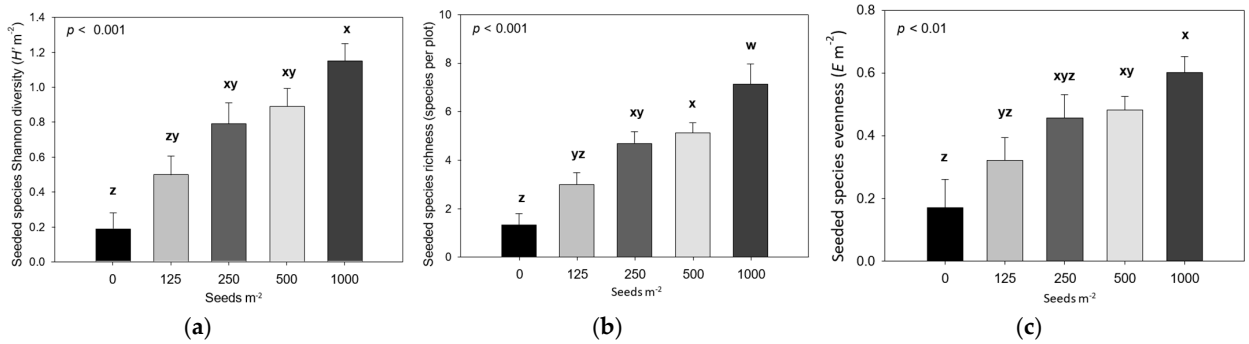


Figure 6. Effects of seeding density treatments on (**a**) the mean Shannon–Wiener diversity index (H' m^{-2}), (**b**) the mean richness (number of species per plot), and (**c**) the mean evenness index (E m^{-2}) of the seeded species community, regardless of year after seeding. Standard errors are plotted with the indices' means averaged from 2006 to 2009. Different letters denote significant differences at $p < 0.05$.

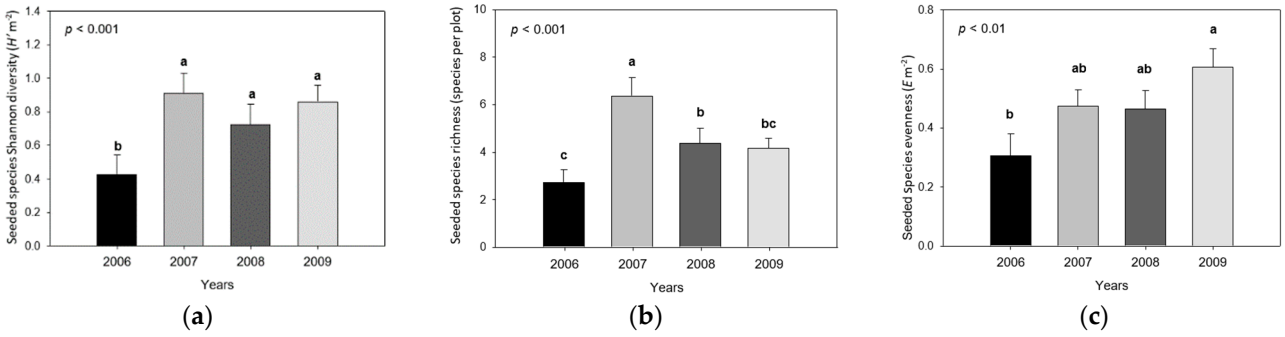


Figure 7. Annual changes in (**a**) the mean Shannon–Wiener diversity index (H' m^{-2}), (**b**) the mean richness (number of species per plot), and (**c**) the mean evenness index (E m^{-2}) of the seeded species community regardless of seeding treatment. Standard errors are plotted with the indices' means averaged across all treatments. Different letters denote significant differences at $p < 0.05$.

Four years later, in 2009, soil properties were assessed within the reservoir, to identify a set of properties that collectively explained the variation in the abundance of the plant species assembled in the reservoir sediments. We determined that in the top 0.15 m of the soil, the mean pH was 7.8 ± 0.05, available phosphorus was 1.6 ± 0.9 ppm, available potassium was 90.3 ± 12.9 ppm, soil Ca was 3732 ± 1333 ppm, soil Mg was 296 ± 20.7 ppm, soil organic matter was 5.9 ± 0.36%, total soil carbon was 3.4 ± 0.30%, total soil nitrogen was 0.23 ± 0.02%, and volumetric soil moisture content was 0.32 ± 0.07 m^3 m^{-3}. The 2009 CCA explained 6.2% of the total variation in the plant community (Figure 12). Together, all the CCA axes explained only 19.5% of the total variance. CCA1 captured 7.4% of the overall variance in the species community, while CCA2 explained 6.6%. Soil available phosphorus and seeding density were correlated (76% and 74%, respectively) with CCA1, but opposite to each other. Conversely, soil organic matter was highly correlated (80%) with CCA2. Of all the soil resources, available phosphorus had the strongest effect on the growth of the perennial grass *Phalaris arundinacea*. Compared to year 2006, the correlation of seeding density (treatment) with CCA1 became stronger in 2009 by 80% and aggregated within seeded species. Of all the environmental conditions considered, seeding density best explained the variation in the seeded plant community in 2009.

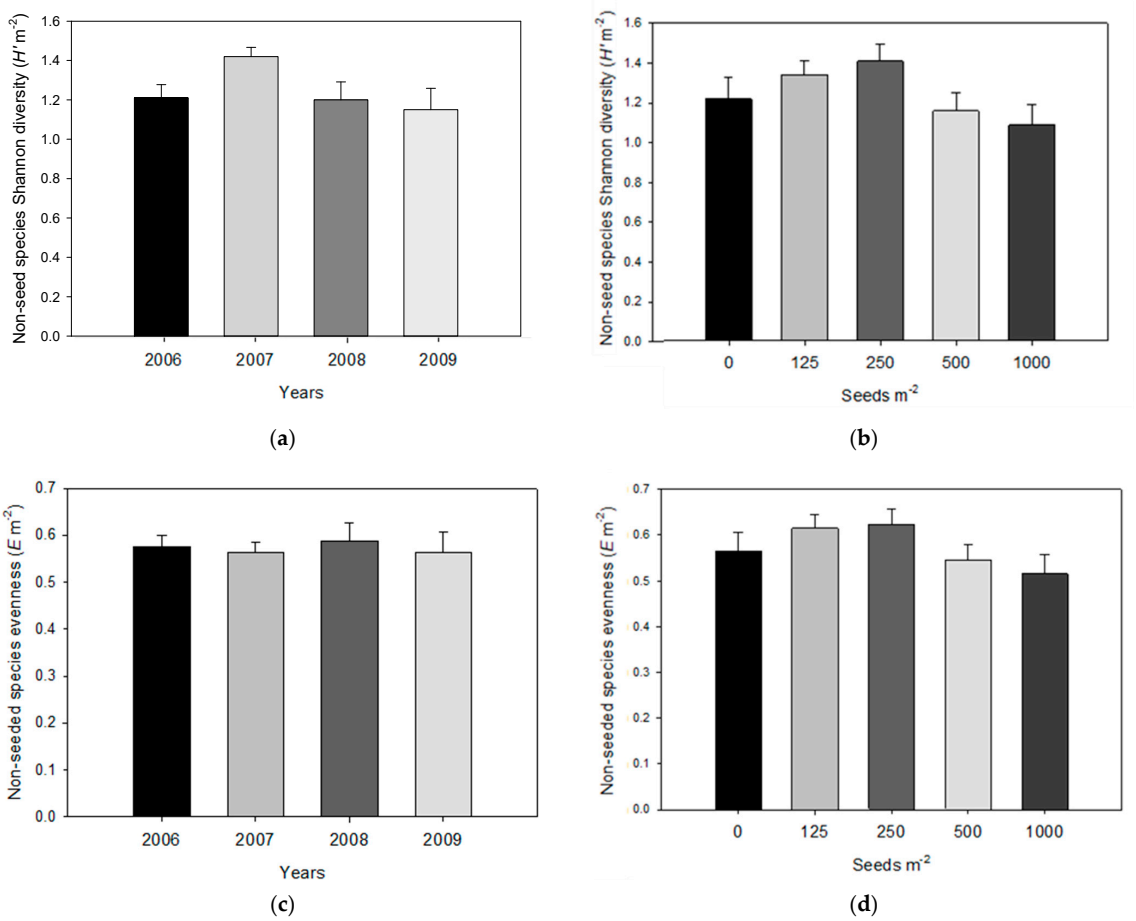


Figure 8. Annual changes in (**a**) the mean Shannon–Wiener diversity index (H' m^{-2}) and (**c**) the mean evenness index (E m^{-2}) of the non-seeded species community regardless of seeding treatment. Standard errors are plotted with the indices' means averaged across all treatments. The effect of the seeding density treatments on (**b**) the mean Shannon–Wiener diversity index (H' m^{-2}) and (**d**) the mean evenness index (E m^{-2}) of the non-seeded plant community regardless of the year after seeding. Standard errors are plotted, with the indices' means averaged from 2006 to 2009.

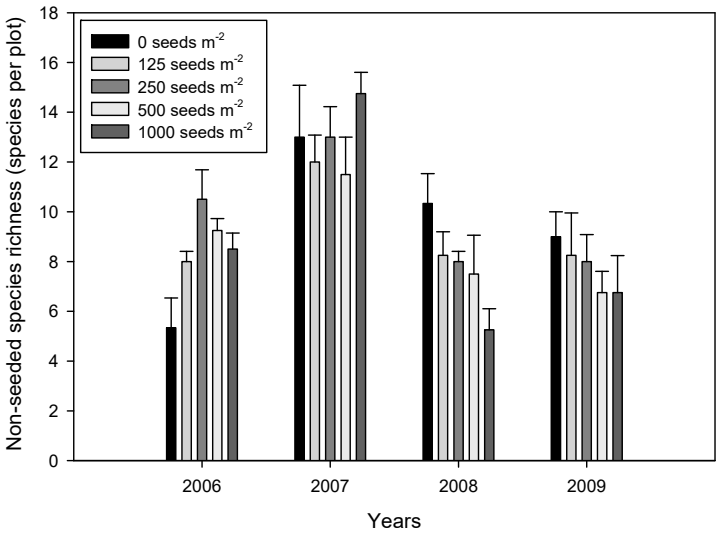


Figure 9. The annual effect of the seeding density treatment on the mean richness (number of species per plot) of the community of non-seeded species. Standard errors are plotted around the species richness means averaged by year and by seeding density treatment.

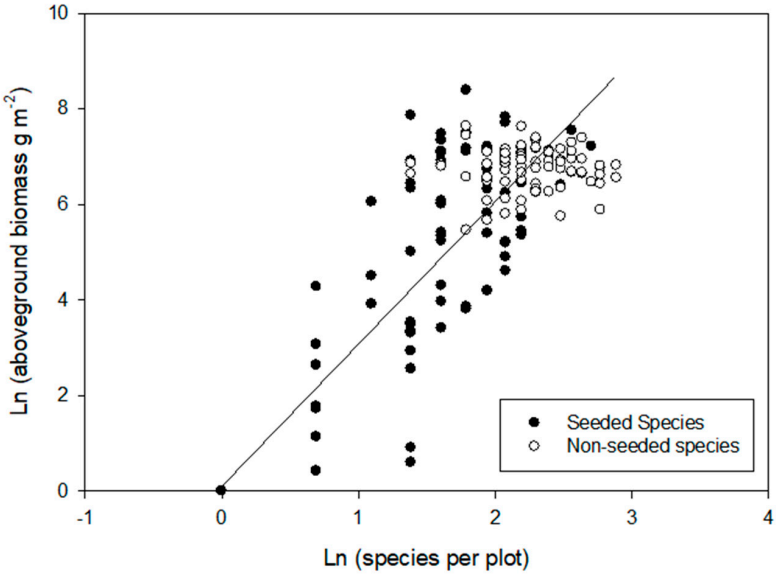


Figure 10. Changes to aboveground biomass (g m^{-2}) of seeded (solid circles) and non-seeded (open circles) species with respect to species richness. The regression line describes the relationship between the natural logarithm of the species richness and the aboveground biomass (g m^{-2}) of the seeded species. The regression equation is ln (seeded species aboveground biomass) = 0.47 + 2.86 ln (seeded species richness); $r^2 = 0.58$ ($p < 0.01$). No relationship existed between the number of non-seeded species and their aboveground biomass ($r^2 = -0.01$ $p = 0.95$).

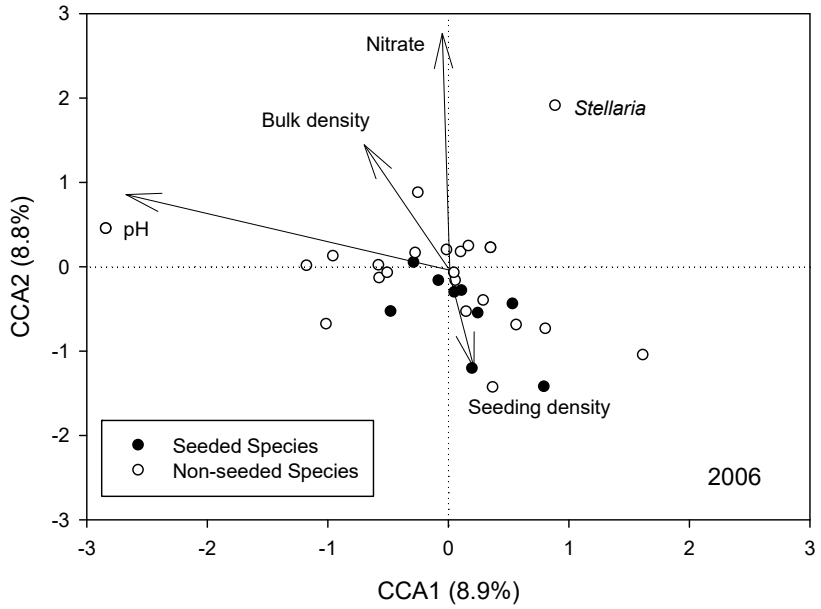


Figure 11. Biplot with results from the canonical correspondence analysis for the plant community and soil conditions in 2006. Seeded species are represented with dark circles, non-seeded species with white circles, and significant environmental variables are represented by arrows. The length of the lines associated with the environmental variables indicates their importance in explaining the species assemblage, and the direction indicates how well species composition and environmental variables correlate. The angle of each arrow indicates the correlation between environmental variables.

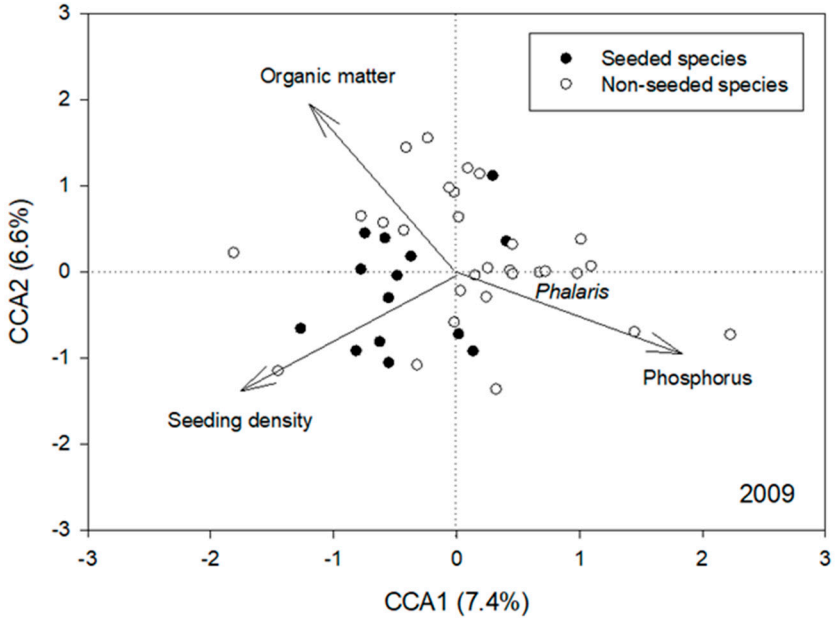


Figure 12. Biplot with results from the canonical correspondence analysis for the plant community and soil conditions in 2009. Seeded species are represented with dark circles, non-seeded species with white circles, and environmental variables are represented by arrows. The length of the arrows associated with the environmental variables indicates their importance in explaining the species assemblage, their direction indicates how well species composition and environmental variables correlate, and their angle indicates the correlation between environmental variables.

4. Discussion

Our data provide compelling evidence that sowing native prairie plants at a higher density into newly exposed sediments expedited the assembly of a native plant community with greater abundance (aboveground biomass) and more diversity in native species. Specifically, sowing 1000 seeds m^{-2} of prairie species increased the aboveground biomass almost three times (288%), and richness more than twice (234%), of the seeded species, compared to seeding only 125 seeds m^{-2} or to no seeding of the sediments. Moreover, four years after seeding, the effect of the higher seeding density treatment not only persisted but was magnified, as the abundance of the seeded plants continued to increase relative to the abundance of non-seeded species in plots seeded with at least 500 seeds m^{-2}. The spatial distribution of the physiochemical properties of the reservoir sediments and the underlying buried soils (described in [3]) also influenced the composition of plant species, especially those that were not seeded. This study is one of the first to test and demonstrate a positive effect of seeding density on the establishment of seeded species within reservoir sediments known to facilitate the rapid colonization of opportunistic plants [17].

The early introduction of native seeds at high rates on the reservoir sediments enabled these species to dominate over time. During the four-year experiment, seeded species became increasingly dominant in the higher seeding density plots ($\geq$500 seeds m^{-2}), reducing the abundance of the non-seeded species by approximately 64%. Priority effects by means of space preemption [58,59] may explain the establishment and dominance of the species, a mechanism demonstrated in other studies [60,61], including seed addition experiments [62,63]. In 2006, one year after seeding, although all the plots were dominated (i.e., the plots had a greater aboveground biomass) by a few non-seeded annual species, the higher-density plots additionally contained numerous seedlings of the seeded species that covered a considerable area, likely limiting the establishment of non-seeded perennials. We assume differences in belowground biomass production between the non-seeded annuals and seeded perennials, even though we did not explicitly measure root production, as above- and belowground allocation patterns among these species are well documented [50].

Fast-growing annual plants typically allocate most plant biomass aboveground, while native prairie plants tend to allocate a large proportion of their biomass belowground [64,65]. Although, initially, the seedlings of the seeded plants produced much less aboveground biomass compared to the annuals, the seeded species likely produced a greater amount of belowground biomass, ensuring their longer-term establishment and competitive advantage. During the three years following seeding, the abundance of the annuals declined, while the abundance of the seeded species increased by more than 20 times in the higher-density plots. We hypothesize that the earlier access to ample space and resources yielded a competitive advantage to the species in the higher-density seeded plots, edging out the non-seeded species that arrived later.

Supporting this hypothesis, results from the control and lower-density plots ($\leq$250 seeds m^{-2}) showed that, despite the early emergence of a few seeded species, non-seeded invasive species suppressed the abundance of the seeded plants in as little as three years. We surmise that, during the four years of the study, interactions between the propagule scarcity of the seeded plants ($\leq$250 seeds m^{-2}) and their unfavorable competition for resources (i.e., space, light, water, and soil nutrients) with non-seeded perennials likely limited their establishment [66]. One year after sowing, seedlings of the seeded species occupied a small area in the low-density plots and could not exploit the resources of the sediments (i.e., they established at low densities), compared to the non-seeded annuals and perennials that proliferated in the bare sediments, allowing them to establish early in the restoration by taking advantage of space, light, and soil resources. In the following years, after the annuals disappeared in these lower-density and control plots, competition favored the non-seeded perennials species because they covered more of the space left by the annual species, which allowed them to consume more resources (i.e., nutrients, water, light), holding down the seeded species. Taken together, these results suggest that the early arrival of the seeded species to the bare sediments, and in large numbers, was critical to their establishment, as it appears important for the seedlings to capture resources and reduce the establishment of non-seeded species.

4.1. Community Composition

We speculate that differences in propagule supply caused the assembled community in the reservoir to separate into two distinct plant communities, which we categorized as "native" and "weedy". Propagule supply from the regional species pool has been recognized as a major factor controlling community composition (e.g., [27,67]), which likely explains the proliferation of the weedy community observed in the control and low-density plots ($\leq$250 seeds m^{-2}). Propagule pressure—the number of propagules and introduction rate of the propagules to a community—has been proposed as an important factor in the colonization of opportunistic species [68] that may, likewise, affect the establishment of native species [20,69–71]. Moreover, some invasive species apparently have a threshold—a number of propagules—such that the establishment of a non-invasive species can only occur when it is introduced at a number greater than the threshold value of the invasive species [72]. Previous studies investigating the influence of *P. arundinacea* propagule pressure on native species establishment found that a propagule pressure threshold existed, beyond which native establishment was unlikely [73]. Although this mechanism has been defined in terms of invading species, it has been suggested that similar mechanisms govern native restoration [74]. Invasive species are not necessarily superior competitors but rather dominate because native species are typically propagule-limited. Accordingly, native species introduced at a number greater than their threshold value, overcoming their propagule limitations, may become strong competitors by lowering resource availability to levels that cause a decrease in invasive species abundance.

The composition of the "native" communities assembled in the high-density plots ($\geq$ 500 seeds m^{-2}) suggests that a seeding density "threshold" may have existed that limited the growth and establishment of non-seeded opportunistic species. We postulate that a threshold value of greater than 500 seeds m^{-2} exists, at which establishment of the weedy

species is limited when sowing occurs early in the restoration of these drained sediments. Inferences beyond this site require additional study; however, because this experiment was performed on a site representative of the region, we speculate that seeding numbers below 500 seed m^{-2} will likely fail in overcoming propagule pressure from invasive plants.

Although we did not experimentally compare the similarity of the "native" communities (>500 seeds m^{-2}) to remnant or restored prairies in the region, the composition of our native community differed from mesic and wet prairies in southern Wisconsin, which are typically dominated by graminoid species amalgamated with a diverse forb layer. The dominant graminoids include big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), prairie dropseed (*Sporobolus heterolepis*), and fox sedge (*Carex vulpinoidea*). Long-term forbs such as prairie blazing star (*Liatris pycnostachya*), compass plant (*Silphium laciniatum*), and butterfly milkweed (*Asclepias tuberosa*) also occur frequently [45]. The four-year prairie community had a paucity of those graminoids and forbs. The composition of the restored prairie community was dominated by a small subset of the seeded mesic prairie species (9 out of 40 species): two short-lived forbs, *Heliopsis helianthoides* and *Monarda fistulosa*, produced 38% of the total aboveground biomass. The plant community also included several non-seeded perennials, of which two species predominated: *Phalaris arundinacea* and *Solidago canadensis*, together, produced 29% of the total aboveground biomass. Based on these results and the recognition that dispersal limitation can result in depauperate plant communities in restored sites, and since restored prairies tend to lose species as they mature [75,76], consideration of a target plant community (and by extension, its functional characteristics) on formerly reservoir sediments may not only require a seeding density greater than its "threshold" but also attention to the composition of the seed mixture (e.g., more long-lived forbs and grasses species).

4.2. Diversity and Productivity

The restored "native" plant community assembled in the drained sediments was also limited by propagules of species endemic to the region. Plots seeded at higher rates showed a greater diversity, richness, and evenness for the seeded plant species, with results comparable to other studies measuring diversity in seeded grasslands [27,69,77]. We hypothesize that space preemption likely explained the effect of seeding density on the diversity of the "native" plant community [58,59] and on the abundance of these plants. In the higher-density plots, the early introduction (i.e., sowing) of numerous seeds facilitated the emergence of an abundance of seedlings of various "native" species [70], which likely reduced competition with non-seeded species that might have been present in the dewatered soil or surrounding area [74]. Consequently, several seedlings of different "native" species survived and became established. These results suggest that numerous species in the seed mixture were good competitors in these newly exposed sediments [78] when dispersed in large numbers. Seeding at high density thus controlled the establishment of undesired non-seeded species, which may give the native plants within these plots a competitive advantage in years to come [29,69]. In contrast, in the low seeding density plots, the establishment of the seeded species was restricted to a few species (less diversity), as they became outnumbered by the non-seeded competitors.

Regardless of seeding density treatment, the Shannon diversity in the "weedy" plant community was similar throughout the experimental sites over the four years of the study. Propagule supply from the seeded species did not overwhelm the establishment of a diverse "weedy" community. We hypothesize that the supply of non-seeded species propagules from the neighborhood was abundant and dispersed rapidly into the bare sediments [79]. Consequently, native species diversity was unable to decrease the diversity of the invasive non-seeded species even in the "native" communities [79,80].

Species richness appears to be a determining factor for the aboveground biomass differences of the native seeded species grown within the reservoir sediments over the four years of the study. There is abundant evidence of the positive relationship between species richness and productivity [81–83] from grassland experiments [53,84,85], as well as from

other ecological systems [86,87]. Although we did not quantify productivity, we found that the more diverse "native" communities (i.e., richness) consistently produced a higher aboveground biomass. A universal mechanism explaining diversity effects on productivity is not indisputable as yet; however, two mechanisms have been proposed. Increased productivity may be driven either by functional complementarity—resource partitioning by multiple species—associated with higher diversity, or by selection effects—few highly productive species contribute to production—at higher diversity [51,88,89]. Although we did not directly test these mechanisms, our four-year seeded plant assemblages either contained species that were comparably better competitors for abiotic resources (i.e., resource efficiency effect), or the high-diversity plots contained highly productive and dominant species for this site (i.e., sampling effect); evidence from this study does not support a complementary resource effect.

The relationship between diversity and aboveground biomass did not hold for the non-seeded species. A redundancy in ecosystem function in the non-seeded species may explain this apparent inconsistency: several, or at least more than one, of the non-seeded species were highly productive during community assembly within the low-density plots and controls [90,91]—conceivably, annual species in the first years of the study and later, perennial species (i.e., *Lactuca serriola* and *Phalaris arundinacea*). We hypothesize that these "keystone" dominant non-seeded species shared similar traits, so the disappearance of one species was not detectable in the overall accumulation of aboveground biomass but maintained a low functionality–neutral diversity productivity relationship, similar to "degraded" ecosystems [90].

4.3. Soil Conditions and Seeding Density Effects on Plant Community

The CCA for the assemblages in 2006 and 2009 relative to soil properties and seeding density revealed that, during the four years of the restoration, the distribution of the seeded species was largely determined by the seeding treatment and less by the physiochemical conditions of the sediments. At the onset of the restoration, seedlings of perennial (seeded and non-seeded) species had only access to resources from the surface sediments and, due to the soil homogeneity of the sediments (see [3]), they likely had to compete first for space and then later for soil resources [92]. Under higher seeding densities, the seeded species covered more space earlier and thus became more abundant, compared to the control and lower seeding density plots. Even though it is likely that some of the seeded species grew roots into the pre-dam buried soils over the duration of this study, we found no evidence that the more heterogeneous physiochemical resources in the buried soils [3] affected the distribution of the plants. Perhaps, as the community continues to mature and shifts allocation from above- to belowground root production and turnover within this buried matrix, the spatial variability of soil resources will create suitable habitats for species with different requirements, and relations between soil resources and the composition of the plant community will emerge [93,94].

In contrast, the CCA analyses suggested that the establishment of a few annual non-seeded species did respond to the spatial distribution [3] of sediment resources. Changes in soil fertility caused by disturbances typically influence the trajectory of plant communities, particularly when nutrient availability promotes the growth of early successional species [95–97]. The 2006 CCA analysis revealed that soil pH and NO3-N affected the plant community assemblage in the first year after seeding, though the effect was small (accounting for 27.6% of the total variance). Three annual plant species dominated all the plots; however, *Stellaria media* covered a substantial area in the southeast side of the former impoundment, where the availability of NO_3-N was approximately two times greater than the mean average of the site (9.6 g m^{-2} vs. 4.1 g m^{-2}). *S. media* grows rapidly in nitrogen-rich soils [98,99]. Thus, under these conditions, the annual species occupied approximately 8.6% of the total aboveground biomass in the sediments of the former impoundment. From these data, we may also infer the effect of a gradient in pH likely associated with the transport of

finer sediments downstream during dam removal [3]; however, a relationship between pH and plant composition was unclear and may be an artifact of the statistical analysis.

In the final year of the study, the influence of soil properties on the plant community decreased (19.5% of the total variance). Interactions between seeding density, available phosphorus, and organic matter appeared to impose the greatest influence on the distribution of all plants, seeded and non-natives, within the community. The first CCA axis indicated a contrast between plots with higher levels of available phosphorus and plots sown at a higher density. Supporting our previous results, the seeded species reached their greater abundance in higher seeding density plots, with the exception of *Aster novae-anglia*, which occurred mostly in plots with lower seeding densities. On the other side, in plots with higher levels of available phosphorus, non-seeded species were more abundant. For instance, the non-seeded perennial grass *Phalaris arundinacea*, the most productive non-seeded plant in 2009, was not only the most abundant species in the lower-density plots (although it also occurred to a much lower degree in plots seeded at the higher seeding densities), it also reached maximum abundance in plots where the concentration of available phosphorus was approximately three times higher than the mean available phosphorus content of the entire site (5 ppm vs. 1.6 ppm). This result is consistent with past studies that concluded that nutrient-rich soils and phosphorus-enriched sediments favored the growth and colonization of *Phalaris* in wetlands and wet prairies (e.g., [100–102]). Although outside the temporal scope of this study, we can only speculate whether *Phalaris* will eventually invade the high-density plots from its clonal centers in the low-density and control plots [42].

While many scientific studies examine the relationship between plant diversity and productivity, most restorations omit ecosystem functioning (e.g., productivity) as their primary goal, focusing instead on social and environmental services such as bio- and functional diversity [34,83]. Collectively, this study demonstrates that applying a diverse seed mix of endemic, native species at a high density can enhance their establishment and increase diversity within formerly impounded sediments, at least in the formative years of assembly. Such differences in seeding density did not entirely inhibit the establishment of opportunistic species but did reduce the competitive edge of non-natives over the four years of this study. Although we did not experimentally compare the similarity of our "native" seeded communities to a remnant prairie, the community composition of our native communities differed in composition and diversity to mesic prairies in Wisconsin, which are dominated by graminoid species with a diverse forb layer [45] and, when disturbed, are typically invaded by reed canary grass [40,42]. The composition of the restored native community included a small subset of the seeded mesic prairie species, dominated by few short-lived native forbs and the invasive *P. arundinacea*; however, *Andropogon gerardii* (big bluestem), the dominant plant in the mesic prairies of southern Wisconsin, was absent in our restored "native" plant community. The root systems of *Andropogon gerardii* and other perennial grasses form complex mats that can potentially reinstall ecosystem functions by enhancing the soil structure and increasing soil organic matter (e.g., [103]). With these results and recognition that restored prairies often change in composition as they mature [75], the consideration of a target plant community (and by extension, its functional characteristics) on drained sediments may not only require a greater percentage of seed but also attention to the composition and functional diversity of the seed mixture, especially in situations where management is prohibitive.

Enhancing grass establishment may require sowing a greater percentage of grass seeds, but restoring diversity and ecosystem functioning may require reconsidering the target plant community (i.e., seeding mixture). This requires identifying the environmental conditions of the restored site, to select a plant community that naturally occurs in the area. For instance, recognizing that the moist conditions of drained sediments may result in a community similar in composition and structure to wet prairies or the wetland communities occurring on river floodplains, sowing seeds of wet-mesic or wet prairie species such as Canada bluejoint grass (*Calamagrostis canadensis*) and cordgrass (*Spartina pectinata*) may

increase grass establishment. Moreover, since these grasses complement each other's phenology—*C. canadensis* is a C3 grass and *Spartina pectinata* is a C4 grass—the canopies of the two grasses may inhibit *P. arundinacea* establishment during the growing season [41,104].

Alternatively, restoration managers may need to consider that seeding native species may not lead to the target plant communities. It is possible that seeding native species at higher densities may not guarantee native species establishment [16] due to propagule pressure from opportunistic species [70] and soil physiochemical conditions [100,105]. In addition, persistent management of the restored site may be necessary to improve the establishment of the seeded native species [106]. For example, periodical removal of opportunistic species (e.g., *P. arundinacea*) may be required, as well as enhancing the establishment of seeded species. The establishment of seeded plants may be increased by sowing a high seeding density of mixtures more appropriate to the soil physiochemical conditions, sowing native species that establish rapidly to limit the colonization of opportunistic species [107] and sowing or re-sowing long-lived perennial species when necessary [108]. An initially higher-cost but potentially more sustainable restoration may also involve restoring or improving the appropriate magnitude and heterogeneity of physiochemical soil properties.

Collectively, this research improves our understanding of the impact that seeding density has on the establishment and diversity of a restored native prairie community in the bare sediments of a former impoundment in southern Wisconsin known to facilitate the colonization of reed canary grass. The study also identifies opportunities for improving the success of the restoration, such as increasing the seeding density, designing a more diverse seed mix, and identifying a seed mix more natural to the new conditions of the disturbed site. A practical result of this study will be to inform restoration managers in their efforts to reinstate native vegetation in similar sites, to guide them to target a plant community appropriate for the site, and make them aware that restored plant communities may differ in composition from those intended. Moreover, acknowledging that highly disturbed sites, such as former impoundments, might never return to their historical condition may encourage managers to reconsider the restoration of some key ecosystem functions, for example, pollination [109], instead of targeting specific plant communities [110]. Finally, understanding the role of belowground conditions that drive community dynamics is important to help reinstate biodiversity and complementary ecosystem processes to disturbed ecosystems [111].

This study provides compelling evidence that sowing native prairie plants at higher densities into newly exposed sediments expedites the assembly of a native plant community with greater abundance and diversity. Sowing 1000 seeds m^{-2} of prairie species significantly increased the aboveground biomass and richness, compared to lower seeding densities or no seeding. Over four years, the effect of a higher seed density persisted and was magnified, with seeded plants outcompeting non-seeded species. The early introduction of native seeds at high rates enabled species dominance over time. This study suggests that seeding density can significantly influence community composition, with a threshold of at least 500 seeds m^{-2} limiting the growth of non-seeded species at this site. Differences in propagule supply resulted in distinct "native" and "weedy" communities, with higher seeding densities favoring native species establishment. Higher seeding densities also promoted diversity and productivity, likely through space preemption and resource competition. Species richness was positively correlated with the aboveground biomass of seeded species; however, diversity did not decrease the diversity of invasive non-seeded species. Together, soil conditions and seeding density affected plant community assemblage. Seeded species distribution was largely determined by seeding treatment, while non-seeded species responded to soil properties, particularly phosphorus levels. Restoration strategies involving diverse seed mixes at high densities may enhance establishment and diversity within formerly impounded sediments, but success depends on soil conditions and management practices. Overall, this research informs restoration efforts by highlighting the importance of seeding density, seed mix composition, and soil conditions in promoting native plant establishment and diversity in dewatered impoundments.

5. Conclusions

This study provides compelling evidence that sowing native prairie plants at higher densities into newly exposed sediments expedites the assembly of a native plant community with greater abundance and diversity. Sowing 1000 seeds m^{-2} of prairie species significantly increased aboveground biomass and richness compared to lower seeding densities or no seeding. Over four years, the effect of higher seed density persisted and was magnified, with seeded plants outcompeting non-seeded species. Early introduction of native seeds at high rates enabled species dominance over time. This study suggests that seeding density can significantly influence community composition, with a threshold of at least 500 seeds per m^{-2} limiting the growth of non-seeded species at this site. Differences in propagule supply resulted in distinct "native" and "weedy" communities, with higher seeding densities favoring native species establishment. Higher seeding densities also promoted diversity and productivity, likely through space preemption and resource competition. Species richness positively correlated with aboveground biomass of seeded species; however, diversity did not decrease the diversity of invasive non-seeded species. Together, soil conditions and seeding density affected plant community assemblage. Seeded species distribution was largely determined by seeding treatment, while non-seeded species responded to soil properties, particularly phosphorus levels. Restoration strategies involving diverse seed mixes at high densities may enhance establishment and diversity within formerly impounded sediments, but success depends on soil conditions and management practices. Overall, this research informs restoration efforts by highlighting the importance of seeding density, seed mix composition, and soil conditions in promoting native plant establishment and diversity in dewatered impoundments.

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