



Soils and Hydrologic Processes Drive Wet Meadow Formation and Approaches to Restoration, Western USA

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Abstract

In 1805, the Lewis and Clark Expedition encountered Nez Perce people at a wet meadow that now holds historical significance to both cultures. Over the past two centuries this northern Idaho site, known as Weippe Prairie, was modified by digging of drainage ditches and introduction of exotic plants for livestock forage. From 2013 to 2017 a restoration was implemented that included filling a drainage ditch and planting five native wetland species. Between 2008 and 2018 we analyzed monitoring well data to quantify water levels through time, soil oxidation/reduction stations to measure redox potential, vegetation plots to track community changes, and pits for soil characterization. Seasonal saturation occurred top-down from direct precipitation and sheet flow over fine-grained soil and a low permeability hardpan approximately 60 cm below ground. Resulting hydrologic effects included a mean water level rise of 23 cm and prolonged growing season saturation. Although the restoration appears to be on a desirable trajectory, two years were insufficient for the wet meadow to transition from dominance by exotic pasture grasses to native wetland species. A combination of recurring monitoring, adaptive management, time, and reevaluation of the physical and ecological processes driving wetland function is required to achieve longterm restoration success.

Keywords Wet meadow · Wetland restoration · Hardpan · Sheet flow · Camas · Weippe Prairie

Introduction

Wet meadows are wetlands with seasonally saturated soils dominated by herbaceous plants, and they are the most

widespread wetland habitat in the western USA (Cooper et al. 2012). In most areas wet meadows have been converted to agricultural land through the use of drainage ditches and planting of exotic agronomic species, particularly grasses. Dewatering a wet meadow facilitates livestock grazing, forage production, and cropping. Restoring degraded wet meadows requires the removal of hydrologic alterations (Patterson and Cooper 2007). However, even after removing previous land uses, irrigation systems, and artificial drainage structures, the legacy effects of vegetation alteration and management may persist. Recovery to pre-disturbance conditions does not occur passively. Restoration requires understanding and recovery of the physical processes that supported formation of the original habitat, and it requires management of the vegetation (Klotzli and Grootjans 2001; Klimkowska et al. 2007; Kołos and Banaszuk 2013).

Interactions among hydrologic regime, soils, and vegetation drive many wetland functions. Hydrologic processes support wetland formation and persistence because the timing, duration, and depth of saturation create a cascade of physical and biological changes driven by soil saturation and anoxia. Soil characteristics including grain size and hydraulic conductivity can strongly influence site hydrologic functioning

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(Cooper and Wagner 2013; Schook and Cooper 2014). Wet meadows are found bordering lakes and rivers (Keddy 2010) as well as in areas with shallow groundwater (Cooper et al. 2012), including where low-permeability soils support periodic flooding.

Over the past 150 years, the introduction and spread of Eurasian grasses has created prairie and wet meadow communities with few species native to North America (Galatowitsch et al. 2000). In addition, wetland drainage and cultivation can reduce the number of seeds and diversity of species in the seedbank (Wienhold and van der Valk 1989). Therefore, wet meadow restoration must address the limited extent of native species on the landscape and competitive dynamics between native and introduced species.

Weippe Prairie is a wet meadow in northern Idaho, USA with important cultural and historical value for both Native and European Americans. The Nez Perce people traditionally gathered in the prairie to socialize, worship, and harvest the tuber of camas (*Camassia quamash* (Pursh) Greene). Members of the Lewis and Clark Expedition first encountered the Nez Perce at Weippe Prairie on 20 September 1805, and the Nez Perce helped nourish the explorers using food derived from camas and dried salmon (DeVoto 1953; Earle and Reveal 2003). Lewis and Clark returned to Weippe Prairie for a lay-over on their return journey eastward in spring 1806 when they wrote of a magnificent camas bloom.

During European-American settlement in the late 19th and early 20th centuries, homesteaders modified Weippe Prairie using a network of drainage ditches that facilitated tillage, hay production, livestock grazing and conifer cultivation. One large ditch artificially drained our study area at Weippe Prairie, likely reducing the duration of seasonal saturation. The site was planted with Eurasian pasture grasses that produced a tall and highly productive vegetation that outcompeted native species. The history of hydrologic and vegetation changes created a site bearing little functional or visual resemblance to what Lewis and Clark experienced. The National Park Service manages Weippe Prairie today with the goals of restoring structure and function of the wet meadow, preserving a culturally significant site, and enhancing the authenticity of the visitor experience.

Our research analyzed the physical and ecological conditions at Weippe Prairie to develop an understanding of current conditions and where appropriate to develop an approach for restoration. The goal was to reestablish hydrologic connectivity throughout the site and enhance the opportunity for remnant native wetland vegetation to reestablish self-sustaining wet meadow vegetation. We addressed the following questions: 1) How have land use history, soils, and hydrologic processes influenced Weippe Prairie? 2) How did the ditch and its hydrologic restoration affect the duration, depth, and movement of near-surface water? 3) How did ditch filling and planting influence vegetation composition? Our approach

included an in-depth soil characterization, nine years analyzing hydrologic processes, earthwork to fill the drainage ditch, and planting wetland species to begin to reestablish native wet meadow vegetation.

Methods

Study Site

Weippe Prairie is 111-ha and located 3 km southeast of Weippe, Idaho (UTM Zone 11 N: 582700 E, 5133480 N; Fig. 1). It is in Nez Perce National Historical Park and within the Weippe Prairie ecological section of the Northern Rockies ecoregion, a gently sloping basalt plateau of mixed conifer forest and shortgrass prairie that supports agriculture, livestock grazing, and logging (McGrath et al. 2002). Weippe Prairie is low-relief and covered by alluvial and lacustrine sediments that are mantled by windblown loess and volcanic ash (Soil Survey Staff 2008) that accumulated during the Pleistocene and Holocene (Lewis et al. 2007). It is predominantly open grassland ranging from 917 to 922 m.a.s.l. and surrounded by mostly level agricultural fields and forested hills. Daily mean low temperature in December is -7.8°C and mean daily high in July is 27.8°C (NOAA NCDC GHCND Station USC00107046, Pierce, ID). Mean annual precipitation is 1078 mm, with 57% falling in November–March when the average is 122 mm/month, while in July–September the average is 39 mm/month.

Since the National Park Service acquired this section of Weippe Prairie in 2004, there has been an ongoing desire to restore the landscape to resemble conditions encountered by the Lewis and Clark Expedition in 1805 and 1806. These efforts have focused on reestablishing high camas densities and the correspondingly spectacular early summer blue-flowered landscape. Camas is a native perennial dicot that grows in wet meadows (Lackschewitz 1991). Successful restoration of Weippe Prairie would accomplish three National Park Service goals: 1) improve the ecological condition, 2) improve visitor experience in this historical setting, and 3) increase the camas population to a density that would allow a modern-day harvest by the indigenous Nez Perce tribal members to reestablish a cultural tradition.

Soil

Weippe Prairie has fine grained soil with low permeability and a hydraulically restrictive subsoil, or hardpan, approximately 60 cm below ground (Fig. 1, right panel). At nine sites a soil pit was dug by hand from which soils were described and sampled using standard methodology (Fig. 2; Schoeneberger et al. 2002). Bulk samples were

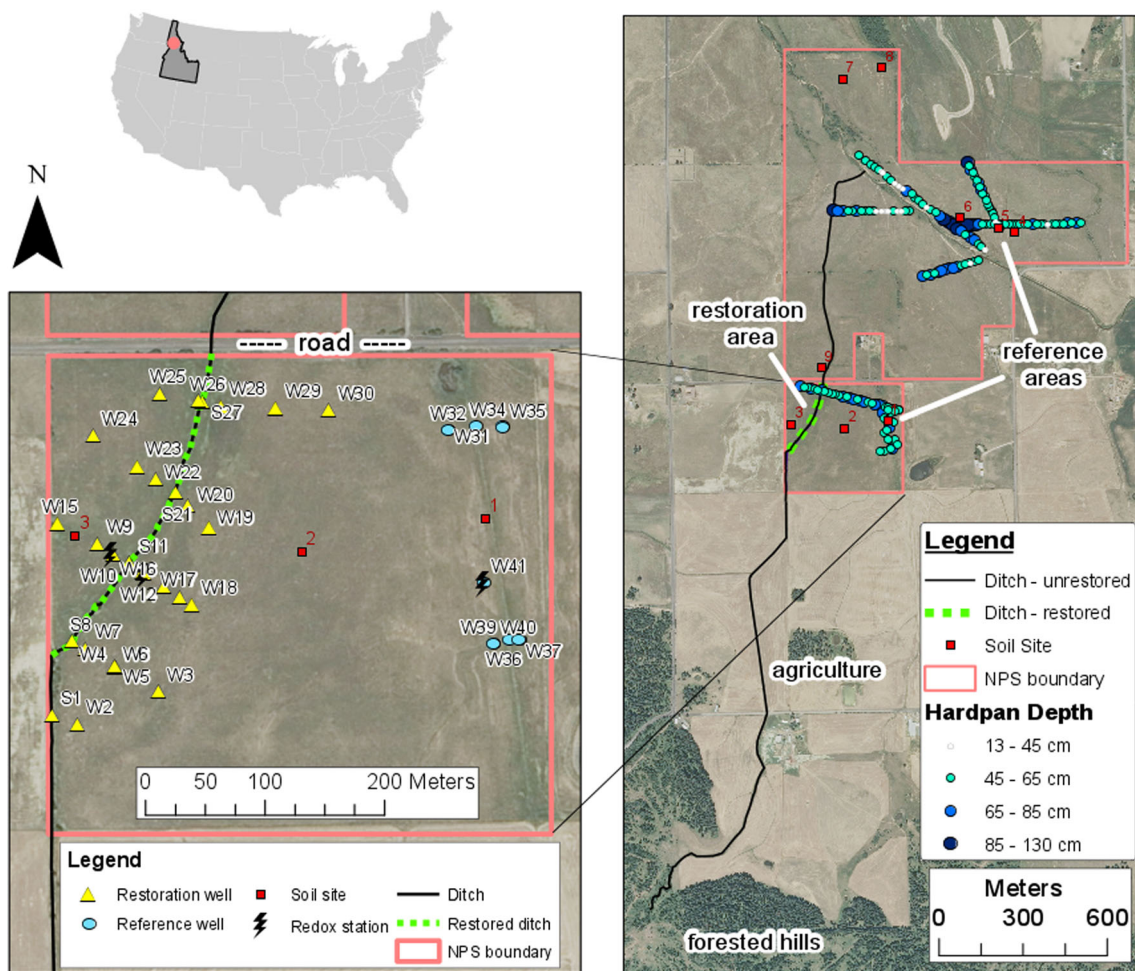


Fig. 1 Map of the Weippe Prairie National Park Service unit in northern Idaho. Right panel shows landscape context with numbered soil sites in red, depth to hardpan along transects, and the north-flowing ditch. Left panel is

the southern unit of the park where the restoration occurred, with wells (w) and staff gauges (s) labeled by number. The town of Weippe, Idaho is 3 km north of the study area

collected from 39 horizons and processed at the Pedology Laboratory, University of Idaho. Samples were air-dried, crushed, and sieved to obtain the <2 mm size fraction that was analyzed for chemical, physical, and mineralogical properties using standard methodology (Soil Survey Laboratory Staff 2004). Physical properties determined were: bulk density, particle-size distribution, texture class, and water retention at tensions of -0.03 and -1.5 MPa to simulate field capacity and wilting point. Chemical analyses performed were: organic carbon content, exchangeable bases, exchangeable acidity, cation exchange capacity, and base saturation (Soil Survey Laboratory Staff 2004; McDaniel and Falen 2011, 2014). The sand fraction of each horizon was observed under a polarizing microscope to determine if it was volcanic ash.

Hydrology

A shallow groundwater monitoring well was installed at each soil sampling site in 2007 ($n = 6$) or 2011 ($n = 3$). Wells were

constructed of 6.4 cm inside diameter PVC pipe that was slotted below ground and solid for the riser. A HOBO water level logger was installed in each soil-site well at a depth corresponding to the hydraulically restrictive soil layer, if present, or ~ 75 cm if not.

In fall 2011 we expanded the hydrologic analysis by installing 43 additional monitoring wells and 13 staff gauges where water levels were measured in 2012, 2013, 2014, 2017 and 2018. Wells were constructed of slotted 3.8 cm inside diameter PVC pipe. Most wells were completed at 45–65 cm below the soil surface, but they ranged from 25 to 114 cm depth. Staff gauges were t-posts installed in ditches and used to measure surface water depth. At eight sites, we installed a nest of 2 or 3 wells completed to different depths to analyze whether a water table existed in the soil or if all water was perched on the surface or above a confining layer. In most years, InSitu Inc. RuggedTroll pressure transducers recorded hourly water levels in nine wells. The remaining wells were hand-measured weekly from late-April through June, then bi-weekly until dry in late-July through mid-September. The

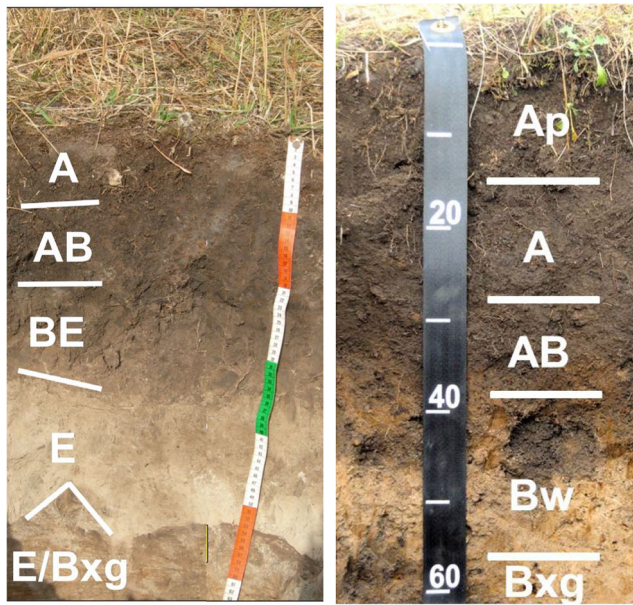


Fig. 2 Top 60 cm of two representative soil profiles, with the sampled horizons identified (horizons described in Schoeneberger et al. 2002). Note that “Bxg” is the hardpan

hand measurements increased spatial resolution and allowed for interpolation.

Comparisons of water levels in reference and restoration areas allowed us to identify the hydrologic effects of restoration. Twenty-five wells and five staff gauges located in or near the restoration area were used to assess the hydrologic effects of ditch restoration, and 18 wells in reference areas were unaffected by the restoration (Fig. 1). Restoration-induced water level changes were compared between 11 May 2012 and 9 May 2017. These dates were selected for three reasons: 1) Annual weather and water levels varied, so comparisons of the same date or period did not necessarily isolate treatment effects, 2) The wells were hand-measured starting in late April, but some wells were dry by May 23 so their record was brief, and 3) Reference well water levels were very similar with only 2.5 cm change between these dates, indicating that any larger changes in restoration wells were treatment-induced.

Soil Oxidation/Reduction

We determined whether Weippe Prairie had long-duration anoxic soils by measuring soil oxidation/reduction (redox) potential at three sites in 2012 and 2013 (Fig. 1). Redox potential is a measure of the electron pressure in a solution, and it quantifies the degree of electrochemical reduction of soils. Reduction of chemicals occurs when they accept a hydrogen or electron, which occurs in the absence of oxygen. Redox values are commonly divided into four categories: oxidized soils ($> +350$ mV),

moderately reduced ($+100$ to $+350$ mV), reduced (-100 to $+100$ mV), and highly reduced (-300 to -100 mV) (Batzner and Sharitz 2006). We consider sites to be oxic if their redox potential was $\geq +350$ mV and reducing if their redox potential was $< +350$ mV. Persistence of anoxic conditions for at least two consecutive weeks during the growing season was used to determine if wetland hydrogeochemical conditions existed at each site.

We measured soil redox potential using pure platinum tipped electrodes. Each electrode was coupled with a Calomel reference electrode, and a Campbell Scientific data logger provided an impulse to both electrodes simultaneously and recorded the difference. Two redox stations were located near the ditch to be filled, and one was at a reference site on the east side of the southern prairie (Fig. 1). At each station, four pairs of electrodes recorded hourly measurements at 20 cm depth.

Vegetation

Vegetation composition was analyzed at all monitoring wells and along line transects in 2012 and 2017. Species canopy cover was visually estimated to the nearest 1% in circular 1 m radius plots around each well and in 1 m² rectangular quadrats placed every 5 m along 25-to-50 m transects that extended perpendicular from the ditch. We analyzed data for 25 plots at wells and 46 plots along transects. Water levels for vegetation plots around wells were obtained from the corresponding well, and water levels for transect quadrats were determined from well data by inverse distance weighting interpolation in ArcGIS. Measurements from 11 May 2012 and 9 May 2017 were used to compare water levels before and after ditch restoration.

A community matrix was generated using the relative abundance of all species in each plot. Bray-Curtis similarity resemblance matrix and a non-metric multidimensional scaling ordination (NMDS) was used to construct a two-dimensional ordination of floristic relationships among samples. A solution for the NMDS ordination was reached in 2 dimensions using the 2012 data after 49 iterations with a stress value of 0.15 and using the 2017 data after 99 iterations with a stress value of 0.13. Environmental factors were analyzed for their correlation to ordination axes ($p < 0.05$). Groups of plots and quadrats with similar floristic composition were identified as communities using a flexible beta (-0.25) cluster analysis with a cutoff level of $h = 1.2$ for 2012 and $h = 1.1$ for 2017. A similarity percentages analysis (SIMPER) identified the species contributing most to the similarities and differences between groups in the cluster analysis. All multivariate analyses were conducted in R and SIMPER analysis was conducted in Primer (Primer-E, Plymouth, UK; Clarke and Gorley 2015).

We measured cover of planted seedlings and volunteer species in the ditch fill zone using the line intercept method. Transects were established every 10 m perpendicular to the filled ditch starting 10 m from the road culvert and extending 280 m upstream to cover the restoration area. The cover of each species was recorded as a percent of transect length, which ranged from 6 to 10 m to match the width of fill.

Restoration

Restoration was conducted in a pilot phase and a ditch filling phase. For the pilot phase we installed three temporary plywood dams across the ditch in September 2012 to simulate ditch filling. Dams were approximately 4 m wide, up to 0.9 m deep, and spaced 75 m apart. Water levels in 2013 and 2014 reflected the dam effect of ponding and diffuse overland flow (Fig. 3). The dams slowed drainage by decreasing the hydrologic gradient between water in the wet meadow and surface water in the ditch.

In October 2015, the entire ditch was filled with imported mineral sediment. The fill extended from the road culvert to the western property boundary, 300 m upstream (Fig. 1). Prior to fill placement the ditch was cleared using an excavator to create a smooth bottom and sides to limit the formation of buried preferential flow paths at undercut banks. Ditch clearing also removed stands of *Phalaris arundinacea* (reed canary grass). Fine-grained mineral sediment was placed in the ditch and compacted with a roller to reduce porosity and erosion. The fill was covered with 15 cm of local weed-free topsoil. Finally, the soil surface was raked by the dozer creating microtopography to facilitate plantings. Native seeds from target wetland species were collected in 2015 and propagated in a commercial nursery. 9,100 seedlings of five common species found in reference sites were planted at 4 seedlings/m²: *Carex microptera* ($n = 2,240$), *Carex nebrascensis* ($n =$

28), *Carex pellita* ($n = 5,872$), *Carex vesicaria* ($n = 320$), and *Scirpus microcarpus* ($n = 640$).

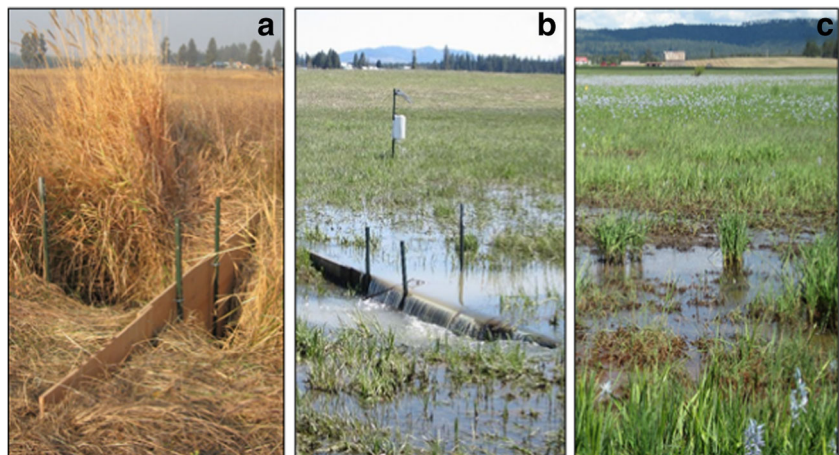
Dump trucks were used to import mineral sediment which was spread and compacted by bulldozers and excavators. Equipment movement compacted the prairie soil adjacent to the ditch. We measured soil strength profiles across the work area to evaluate if vehicles affected soil compaction, which has implications for plant growth. We compared soil density within the ditch fill zone, native soil areas that were compacted during filling, and undisturbed reference prairie areas. Soil density was measured from the ground surface to 45 cm depth using a Spectrum Technologies, Inc. FieldScout SC 900 soil compaction meter. This penetrometer measured density in 2.5 cm depth increments at 70 locations along two transects perpendicular to the former ditch. Measurements were made just after ditch filling in October 2015 and after two growing seasons in August 2017. Differences among treatments were identified for each depth using Dunn's Kruskal-Wallis test for multiple comparisons, with significance at $p < 0.05$ reported for compacted and fill zones compared to the reference prairie.

Results

Soil

In all nine soil pits we found redoximorphic features including low-chroma colors, iron concentrations, and depletions caused by seasonal saturation (Vepraskas 2001). Expression of these features varied among the sites and reflected both the duration and depth of saturation. Silty clay loam, silty clay, and clay textures dominated the subsoil horizons, with one site containing 85% clay. These textures are typical of soils in alluvium, loess, and lacustrine sediments. The fine-grained sediment suggests deposition in a former lacustrine

Fig. 3 Photographs of the restored ditch. **a** is the ditch in fall 2012, with a newly installed plywood dam spanning the ditch prior to any hydrologic or vegetation restoration. **b** is an opposite view of the same dam causing the overbank flow during spring runoff, with the redox station near well 12 in the background. **c** is the filled ditch in May 2017; the blue flower in the foreground and background is camas



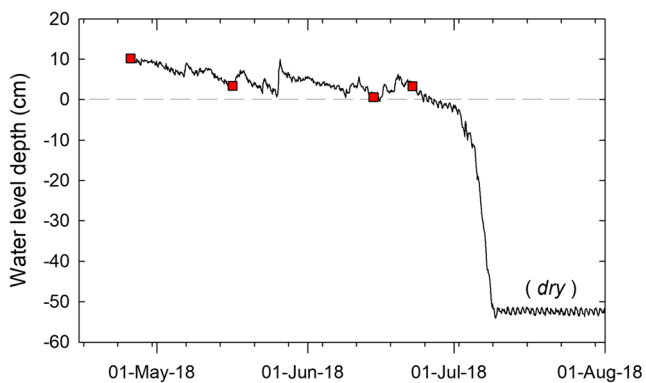


Fig. 4 Water level in restoration area well 28 in 2018, as recorded every 2 h by a groundwater pressure transducer (line) and hand measurements (red squares). Dashed gray line is ground surface

environment, an interpretation supported by the presence of diatoms in the coarse silt fractions of some samples.

A hydraulically restrictive horizon is a key feature of Weippe Prairie soils and was identified at seven of the nine sites. Bulk densities of near-surface soil horizons were 1.1–1.4 g/cm³, which is in the range considered acceptable for plant growth. However, at most sites subsoil bulk densities exceeded 1.5 g/cm³ that is known to restrict root growth (Brady and Weil, 2010). These restrictive subsoil horizons were identified by the exclusion of plant roots from the soil matrix, brittleness, abrupt textural and/or structural differences, and excavation difficulty. These horizons can prolong saturation because soil water moves at very low to moderately low rates of <1.5 mm/h (Soil Survey Staff 2008).

All surface horizons were acidic with pH ranging from 3.7–5.0, reflecting relatively high exchangeable acidity in surface horizons and low base saturation. The pH in all sites increased with depth. Carbon content of the A horizon ranged from 3.2 to 5.0%. This is likely due to seasonal saturation and relatively cold temperatures that limit root and litter decomposition. Quantities of exchangeable bases (Ca²⁺, Mg²⁺, K⁺) were similar across the soils and considered sufficient to not limit plant growth.

Hydrology

In contrast to most wetlands in the western USA, Weippe Prairie is surface water-driven with low-permeability soil that promoted near-surface saturation in spring and early summer in all study years. Sheet flow, or overland flow, occurs because the hydraulically-restrictive soil and low-relief landscape resist channel formation, causing runoff to be shallow and diffuse as it moves across the vegetated land surface. Free water occurred seasonally above the hardpan layer that is approximately 60 cm below the soil surface. Relatively small summer rain events caused large water level rises, surface water ponding, and sheet flow, all factors that prolonged plant-available water. Surface and near-surface water ceased to occur after inputs from the watershed stopped. In 2018 standing water occurred through late June at restoration well 28 but in early July the water level declined by 39 cm in three days (Fig. 4). The relatively level topographic gradient, low transpiration demands, and very low soil hydraulic conductivity should produce a much slower water table decline than 13 cm/day. The precipitous decline indicates that water in the well casing was from surface water, not groundwater, and soil below the surface was unsaturated. After surface water inputs ceased, water in the monitoring wells that extended below the hardpan quickly infiltrated the unsaturated zone and the well went dry. This occurred during every year of our study. The hydrologic system apparently crosses a threshold when drainage surpasses inputs and retention, after which the prairie can no longer support perched surface water. Winter re-wetting occurred just as rapidly as summer drying (Fig. 5). Pondered conditions varied from 0 to 187 days in the wells associated with soil study sites (Table 1).

Soil Oxidation/Reduction

Soil redox potential closely tracked variation in soil saturation, and anoxic conditions occurred when soil within

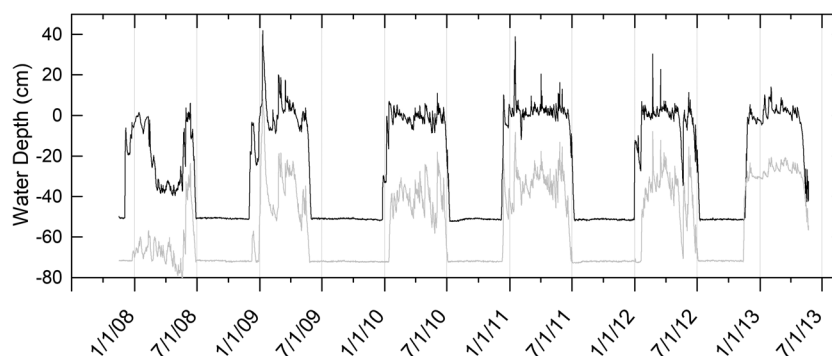


Fig. 5 Water levels for 2008–2013 for wells at reference soil site 1 (black line) and a location that would be restored, soil site 3 (gray line). Although condensed on this six-year x-axis, the drawdown was slightly delayed at

site 3 relative to site 1 in the 2013 pilot restoration year. Flat lines from late summer into winter indicate a dry well. Annual vertical gridlines are January 1 and July 1

Table 1 Number of days with ponded water and a measureable water table within ~75 cm of ground surface (i.e., perched on the hardpan) for wells at soil sites for water years 2009–2013. Note that site 3 in 2013 was the only site potentially affected by restoration actions

Soil Site Well #	2009		2010		2011		2012		2013	
	Water table	Ponded	Water table	Ponded	Water table	Ponded	Water table	Ponded	Water table	Ponded
	Number of days									
1	181	79	196	71	213	153	191	98	197	103
2	156	0	163	0	193	0	150	0	166	0
3	158	5	171	0	201	0	163	0	200	0
4	191	140	176	129	229	187	190	149	341	148
5	197	79	198	28	245	18	211	19	336	0
6	172	0	164	0	204	0	163	0	195	0
7	—	—	—	—	—	—	122	0	131	0
8	—	—	—	—	—	—	207	5	356	36
9	—	—	—	—	—	—	142	0	141	0

Fig. 6 Redox potential, water levels, and precipitation at three locations in 2012 and 2013. The top two panels were near the restored ditch. Well 41 (third panel) is in a reference area on the prairie's eastern side in an area of high camas density. Dashed gray lines are at 350 mV and lower numbers indicate reducing conditions. The bottom panel is daily precipitation

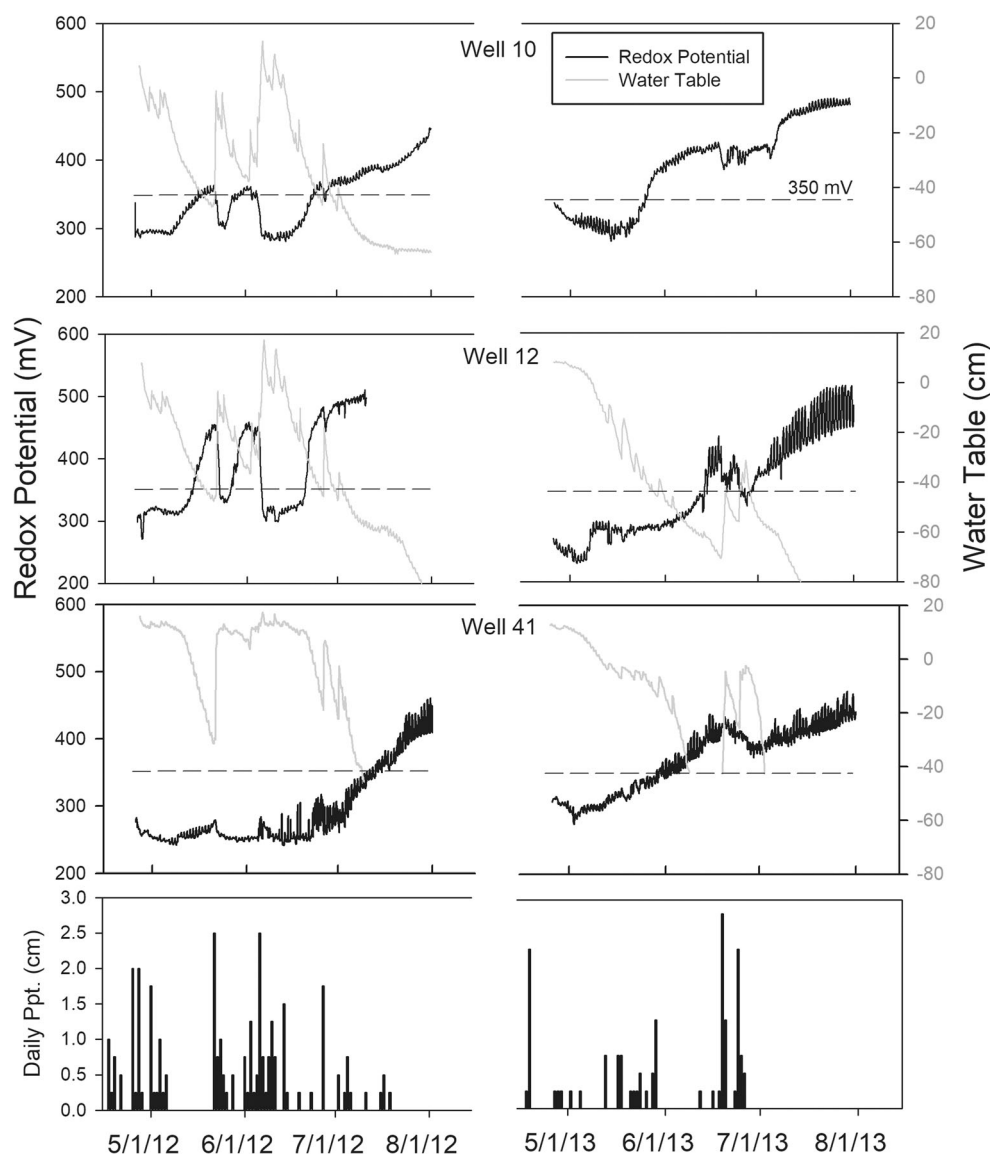


Table 2 Pre-restoration plant communities identified using cluster analysis for 2012. The post-restoration communities for 2017 and described later are also included

Survey year	Plots (n)	Community name	Dominant species
2012	23	Alopra	<i>Alopecurus pratensis</i>
2012	16	Phlpra-Alopra	<i>Phleum pratense</i> <i>Alopecurus pratensis</i>
2012	12	Alopra-Astsp.	<i>Alopecurus pratensis</i> <i>Aster</i> sp. <i>Phleum pratense</i> <i>Agrostis gigantea</i>
2012	12	Broine-Poacom	<i>Bromus inermis</i> <i>Poa compressa</i>
2012	8	Phaarua	<i>Phalaris arundinacea</i>
2017	10	Phaarua	<i>Phalaris arundinacea</i>
2017	17	Alopra-Phaarua	<i>Alopecurus pratensis</i> <i>Phalaris arundinacea</i>
2017	27	Alopra	<i>Alopecurus pratensis</i>
2017	3	Gnapal	<i>Gnaphalium palustre</i>
2017	3	Junbuf-Junens	<i>Juncus bufonius</i> <i>Juncus ensifolius</i> <i>Gnaphalium palustre</i> <i>Eleocharis</i> species
2017	7	Broine-Alopra	<i>Bromus inermis</i> <i>Alopecurus pratensis</i>
2017	4	Phlpra-Forb	<i>Phleum pratense</i> Unknown forb <i>Alopecurus pratensis</i> <i>Bromus inermis</i>

20 cm of the ground surface was saturated. Anoxic conditions occurred in early summer of 2012 and 2013 at all three measurement sites (Fig. 6). Well 10, located near the drainage ditch, had a redox potential that remained <350 mV from early May 2012 through late June 2012. Redox potential responded to the water level as the prairie wetted and dried in June. Well 12, also located near the drainage ditch, had a redox potential <350 mV when the water level was within 20 cm of the soil surface. Reference area well 41 had a water level near the soil surface until early July and the redox potential was <300 mV until that time, indicating prolonged anoxic soil conditions in the reference area that was far from the ditch. In 2013 the soils remained anoxic until late May, a shorter period than in 2012 due to little early summer precipitation in 2013. These data indicate that all three areas of Weippe Prairie had anoxic soils early in the growing season for a sufficient duration (at least two consecutive weeks) to create wetland hydrologic conditions.

Pre-Restoration Vegetation

In 2012, 43 vascular plant species occurred in five communities identified using cluster analysis. Communities were characterized by the one or two species that contributed the greatest proportion of within-community similarity (Table 2; Appendix Table 3). The plots ordinated along the two major NMDS ordination axes, corresponding to water level ($r^2 = 0.42$; $p = 0.001$) and *Camassia quamash* (camas) cover ($r^2 = 0.10$; $p = 0.03$; Appendix Fig. 12). The most abundant community was dominated by the exotic grass *Alopecurus pratensis* and occurred at an average water level on 11 May 2012 of −13 cm relative to ground surface (se = 3.0 cm). The second most common community was dominated by *Phleum pratense* and *A. pratensis*, and it occurred at an average water level of −29 cm (se = 2.7 cm). A community dominated by *Bromus inermis* and *Poa compressa* occurred in the driest areas with an average water table of −37 cm (se = 3.4). The *Alopecurus pratensis* – *Aster* spp. community had the highest species richness. The *Phalaris arundinacea* community occurred where the May water level was closest to the surface but seasonally variable (avg. = −7 cm, se = 6.2).

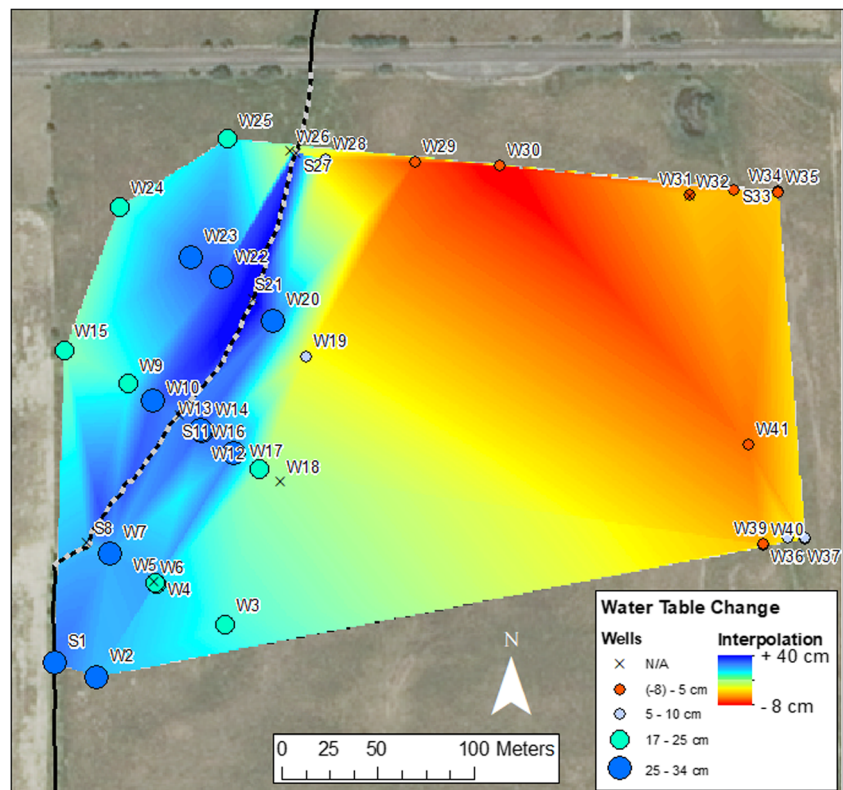
Restoration

Hydrologic Response

Filling the ditch created higher and more prolonged near-surface water levels in 2017 and 2018 compared to the pre-restoration year 2012 or pilot restoration years 2013 and 2014. Both the pilot and permanent hydrologic restorations raised water levels at least 86 m from the ditch. Water levels in restoration area wells averaged 26 cm higher in 2017 than 2012 (se = 1.6 cm; range = +6 to +32 cm; Fig. 7), while water levels in reference wells were 2.5 cm higher in 2017 than 2012 (se = 0.8 cm; range = −7 to +8 cm). This indicated a 23 cm average water level rise due to ditch filling. The water level increase was greatest closest to the filled ditch (Fig. 7).

The pre-restoration year 2012 had more summer rain than the five post-restoration years (Fig. 8a), and reference wells had higher water levels from late-April through early-May compared to 2018 (Fig. 8c). In contrast, wells in the restoration area had their lowest early summer water levels in 2012 (Fig. 8d). Well 17, which was in the restoration area but far from the ditch, had a similar early summer water level in all years (Appendix Fig. 11). This indicated that distance from and elevation above the ditch limited hydrologic changes from restoration. After May 23, the highest water level in reference wells occurred in 2012. However, 2012 had the highest post-May 23 water level in restoration area wells for only 10–

Fig. 7 Water level differences between 2012 and 2017. Circles are scaled to magnitude of change, with small red circles having little change and large blue circles being roughly 30 cm higher in 2017. The surface interpolates water level changes, which ranged from little change (red) up to a 40 cm increase (blue). Note the contrast between the restored ditch area (left) and the reference area (right)



12 days, following rain events (Fig. 8d). Although 2012 had the highest summer precipitation, 2013–2018 had higher water levels in the restoration area. Overall, ditch filling achieved the desired effect of delaying runoff, prolonging saturation, and extending the duration of growing season plant-available water.

Soil Compaction

The filled, compacted, and reference soils had different soil strength profiles immediately after ditch filling but were similar after two years. In 2015, heavy machinery traffic led to a compacted area strength averaging 1955 kPa in the upper 20 cm of soil compared to 1512 kPa in reference areas, with significant differences at 2.5 to 7.5 cm depth (Fig. 9). The fill zone was like the reference prairie at 0 to 27.5 cm depth but more compacted below 30 cm, a difference that was significant at 35 cm. The high strength below 30 cm (mean = 3702 kPa) was below the primary rooting depth and helped prevent piping in the restoration area. The compacted prairie was similar to the reference prairie in 2017. This recovery occurred after two annual cycles of freezing, thawing, and saturation. Additionally, after two years the fill area soil strength decreased in the initially dense zone below 30 cm (mean = 2472 kPa). The fill at 17.5 cm depth was significantly less dense than reference prairie, but

this was inconsistent by depth. Overall, convergence among the three zones after two years suggests that the unnatural strengths identified immediately after construction returned to natural levels with time.

Vegetation

The most common plant community after restoration was still dominated by the Eurasian grass *Alopecurus pratensis*. It occurred where the early May 2017 water table averaged +5 cm (se = 1.7; Fig. 10). The second most common community was dominated by *Alopecurus pratensis* and *Phalaris arundinacea* and occurred at an average water level of -9 cm (se = 4.0). Areas with the deepest water tables were dominated by *Bromus inermis* and other upland species. The intact prairie plots had minor species composition differences between 2012 and 2017, indicating that the time since restoration was insufficient for the desired changes. In contrast, where we filled the ditch a complete change in species composition occurred because we removed *Phalaris arundinacea*, imported fill, and planted native species. The Gnappal and Junbuf-Junens communities developed on the fill and had the highest percent cover of native species of any community. Across all plots and communities, native plant cover increased from 6% (se = 1.1%) in 2012 to 8%

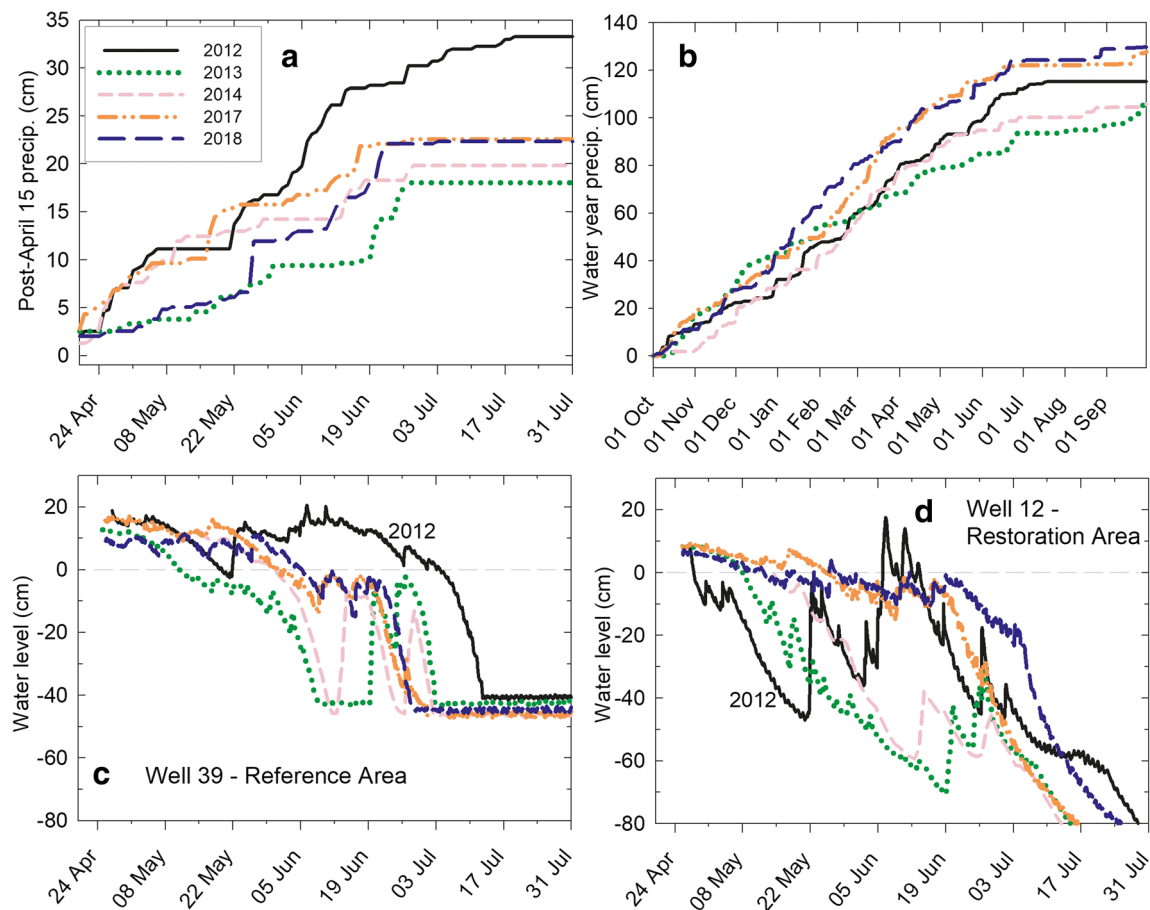


Fig. 8 **a** Growing season (Apr 15 - Jul 31) and **(b)** water year precipitation for study years 2012–2018. Water levels are shown for **(c)** well 39 from the reference area, and **(d)** well 12 from the restoration area. 2012 (black solid line) was before restoration and had the highest summer rain **(a)**, but precipitation was average for the entire water year **(b)**. 2017 and 2018 had average summer but high water year precipitation. Note the relative

position of 2012 water levels for reference vs. restored areas: **(c)** it was usually highest for the reference area, but **(d)** plywood dams raised early-season water levels (2013–2014), and the ditch filling maintained high water longer (2017–2018). Note that the roughly horizontal data at bottom in **(c)** means the well was dry. Three more wells are shown in Appendix Fig. 11

($se = 2.3\%$) in 2017, and exotic plant cover decreased from 76% ($se = 2.4\%$) to 73% ($se = 4.0\%$).

Camassia quamash, a key native target species for restoration, occurred in 41 of 71 plots in 2012 and in 2017, 27 of which were the same plots. *C. quamash* cover averaged 1.5% in 2012 and 1.9% in 2017. It occurred where the water level in early May 2012 varied from +7 to −57 cm (mean = −22 cm) and from +21 to −45 cm in 2017 (mean = −2 cm).

After two growing seasons, cover of the five planted native species was 13%. Sixty-four percent of planted seedlings were *Carex pellita*, and it comprised 50% of total planted species cover. Twenty-five percent of planted seedlings were *Carex microptera*, and it comprised 22% of the cover. Seven percent of the seedlings planted were *Scirpus microcarpus*, yet it provided 24% of planted species cover. Four percent of seedlings planted were *Carex vesicaria*, and it provided 4% of total planted species cover. *Carex nebrascensis* seedlings were sparsely planted (0.3%), but none were recorded on the sampled transects. Including the planted species, 15 species

contributed to the total plant cover of 77% along sampled transects, with the remaining 23% being bare ground. *Agrostis exarata*, a desirable native perennial bunchgrass, was the most abundant opportunistic species to establish on the fill. This species colonizes recently disturbed sites and is important in early seral stages (Klinka et al. 1985). *Juncus bufonius* was also abundant and is a desirable annual pioneer species that rapidly establishes to stabilize soil and will not compete with the establishment of later seral species.

Discussion

Prior to restoration, measured water levels and redox potentials at Weippe Prairie indicated that the hydrologic regime was that of a wetland. However, due to drainage and land use changes, the duration of saturation had been reduced and the species composition changed after

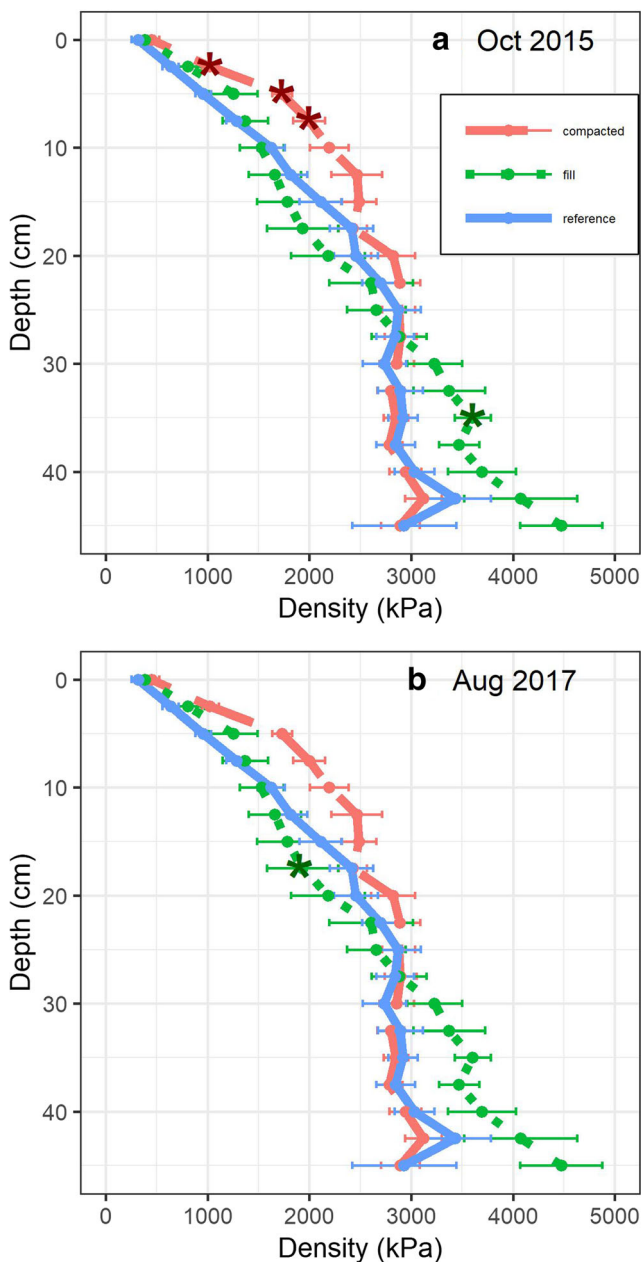


Fig. 9 **a** Soil strength by depth immediately after ditch filling and **(b)** two years later. Lines are mean and standard error for the filled ditch zone (“fill”, green-dotted), the heavy machinery driving zone (“compacted”, red-dashed), and the surrounding reference prairie that was unaffected by construction (“reference”, blue-solid). Significant difference from reference is denoted with an asterisk (*)

the introduction of European pasture grasses. Hydrologic restoration increased surface water retention, the duration of soil saturation, and plant-available growing season water. These changes are likely key to restoring the natural landscape, but other measures such as additional vegetation management may be required to fully achieve the desired conditions in this altered landscape.

Weippe Prairie historically had a sheet flow hydrologic system created by very low soil hydraulic conductivity

and low gradient topography. This contrasts with most wetlands in the western USA, which are supported by a water table that is connected from the bottom to a larger groundwater system (Cooper et al. 2012). Similar sheet flow hydrologic systems can occur on sites with very high clay content soils (Cooper and Wagner 2013). The absence of connection to the deeper groundwater flow system accentuates the importance of restoring ditches in wet meadows.

Wet meadows throughout the world have been modified by intensive human land uses that fundamentally altered their character and function (Tiner 1984). This includes widespread conversion to livestock forage production when sufficient water arrives from precipitation and/or irrigation (Sueltenfuss et al. 2013). Hayfield creation historically has included plowing and introducing Eurasian pasture grasses including *Alopecurus pratensis*, *Phleum pratense*, *Agrostis gigantea*, *Bromus inermis*, *Poa pratensis*, *Poa compressa*, and *Phalaris arundinacea*. These exotic grasses proliferated not only because they possess invasive traits but because land management, such as long-term grazing or hydrologic alteration from drainage ditches, supports their persistence (Norton et al. 2007). These species dominate Weippe Prairie today, and even after hydrologic restoration the vegetation more closely resembles a meadow native to central Europe than to the western USA. *Phalaris arundinacea* (reed canary grass) is a particularly invasive species that has proliferated in wetlands across the northern USA, negatively impacting native species richness and abundance (Galatowitsch et al. 1999; Spyreas et al. 2010). Certain genotypes of *P. arundinacea* are native to the USA, and it was collected by the Lewis and Clark Expedition in Montana (Earle and Reveal 2003). However, a Eurasian ecotype introduced early in the twentieth century is highly invasive (Maurer et al. 2003) and can outcompete native wetland species, and at Weippe Prairie *P. arundinacea* and camas occupy similar habitats. Competition between the two species was not assessed in this study, but the tall monotypic stands of *P. arundinacea* indicate it is a superior competitor once established.

As expected, the floristic composition of Weippe Prairie did not shift to that of a native wet meadow two years after hydrologic restoration, and camas density was unchanged. An analysis of nearly 40 years of data in European wet meadows found that post-restoration communities often proceed along unanticipated successional pathways because of altered nutrient availability, intrinsic species fluctuations, and species invasions (Klotzli and Grootjans 2001). Rewetting alone is often insufficient to result in increased native species cover and richness in wetlands (Klimkowska et al. 2007; Cooper et al. 2012). Instead, species composition can improve if rewetting is combined

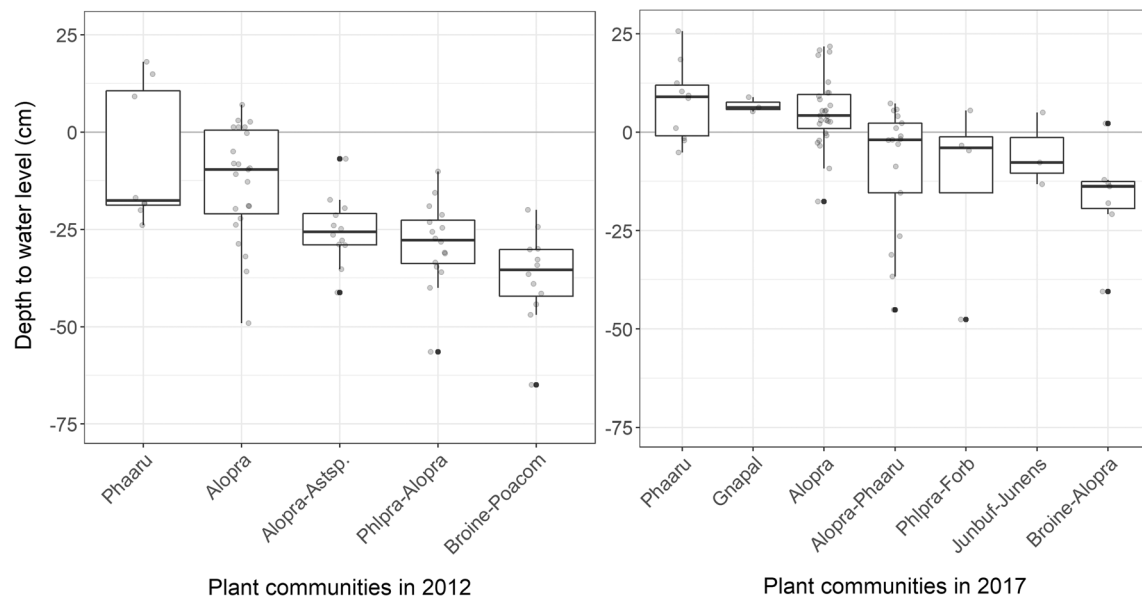


Fig. 10 Depth to water (cm) in May 2012 (left) and 2017 (right) for plots in plant communities identified from similarity, ordination, and SIMPER

analyses. Ground surface is 0 cm. Community names and their common species are identified in Table 2

with species introductions or topsoil removal to eradicate invasive species and their seed banks (Klimkowska et al. 2007). At Weippe Prairie, we rewetted the soil, removed topsoil that supported *P. arundinacea*, and planted native wetland species. However, at this scale the restoration is likely to occur over decades, not two years.

Our actions occurred locally, but watershed-scale factors also affect restoration success. For example, afforestation upgradient in the watershed can increase transpiration and reduce inflows (Klimkowska et al. 2010). Ditching upstream of our study site likely increased inflow by reducing upstream water retention and evapotranspiration. Livestock production in the watershed may alter nutrient influxes and affect competition. Additionally, climate change can limit the persistence of wetland conditions that occurred in the past (McMenamin et al. 2008; Schook and Cooper 2014). These complex landscape variables influence wetland processes at Weippe Prairie, and their interacting influence will affect the restoration.

The native species we planted established and grew, and a larger effort could result in significant vegetation changes. Planting additional native clonal species, such as *Carex pellita*, could push the vegetation from exotic grasses toward native species. Camas is found in areas dominated by exotic grasses today, but its distinctive growth form and seasonality are unlikely to allow it to outcompete the grasses. We were unable to identify consistent relationships between camas density and soil characteristics or water levels. Instead, Weippe Prairie camas density is likely due to other factors such as past management, competition, disturbance, and nutrient availability (Klotzli and Grootjans 2001).

Because wet meadows have a seasonally saturated hydrologic regime, even small ditches can reduce the

hydroperiod and cause significant impacts. This is especially true at sites like Weippe Prairie, where multiple shallow ditches reduced or eliminated sheet flow needed to sustain top-down soil saturation. Wet meadow restoration often also includes reestablishing hydrologic connectivity disrupted by roads. At Weippe Prairie, a road bisects the wet meadow and has only two culverts that focus water into channels. After concentrating flows, it is very difficult to recreate sheet flow. One option to reduce flow concentration is to install permeable road bases that allow surface flow through coarse road bed material rather than being channeled into culverts (Zeedyk 1996). Additional restoration measures at Weippe Prairie could improve wet meadow function and create a more authentic visitor experience for this culturally-significant historic site.

This study illustrates the value of carefully investigating the soil characteristics and hydrologic processes that support wetlands before selecting restoration priorities and approaches. Pilot restorations can test the efficacy of restoration approaches, and approaches can be adapted through time as effects unfold. Considering the immense geographic scale of wetland conversions, it is critical to understand the processes that drive different wetland types and develop a range of restoration techniques to restore degraded wetlands.

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Appendix

Supplemental Figures

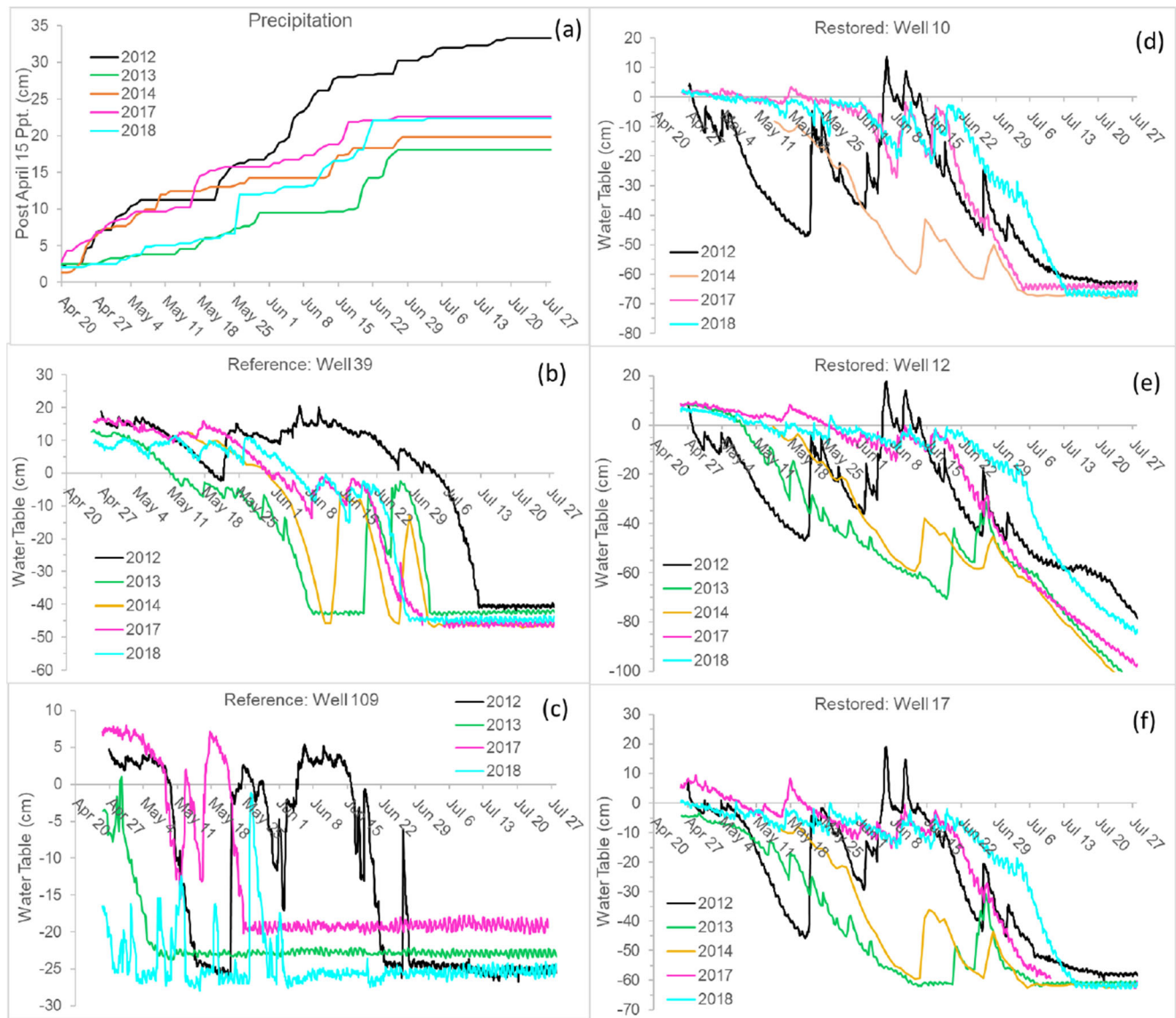


Fig. 11 Expanded version of Fig. 8 with additional data from wells 10, 13, and 109. Reference wells on the left side (b, c) show that the pre-restoration 2012 had the highest water levels because of high summer rain

(a). In contrast, for the restored area wells at right (d, e, f) the years following restoration had higher water levels

Fig. 12 Non-metric multidimensional scaling (NMDS) ordination of plots sampled in 2012. Colors indicate communities determined by flexible beta cluster analysis and classified by the species that contributed the greatest proportion of similarity within groups, as determined by SIMPER analysis. Environmental variables of water level and *Camassia quamash* percent cover (CamasPC) are shown as vectors and were determined to be significantly correlated to projected plots. Presented species are dominant and show their distribution relative to communities (Broine = *Bromus inermis*, Phaaru = *Phalaris arundinacea*, Alopra = *Alopecurus pratensis*, and Phlpra = *Phleum pratense*)

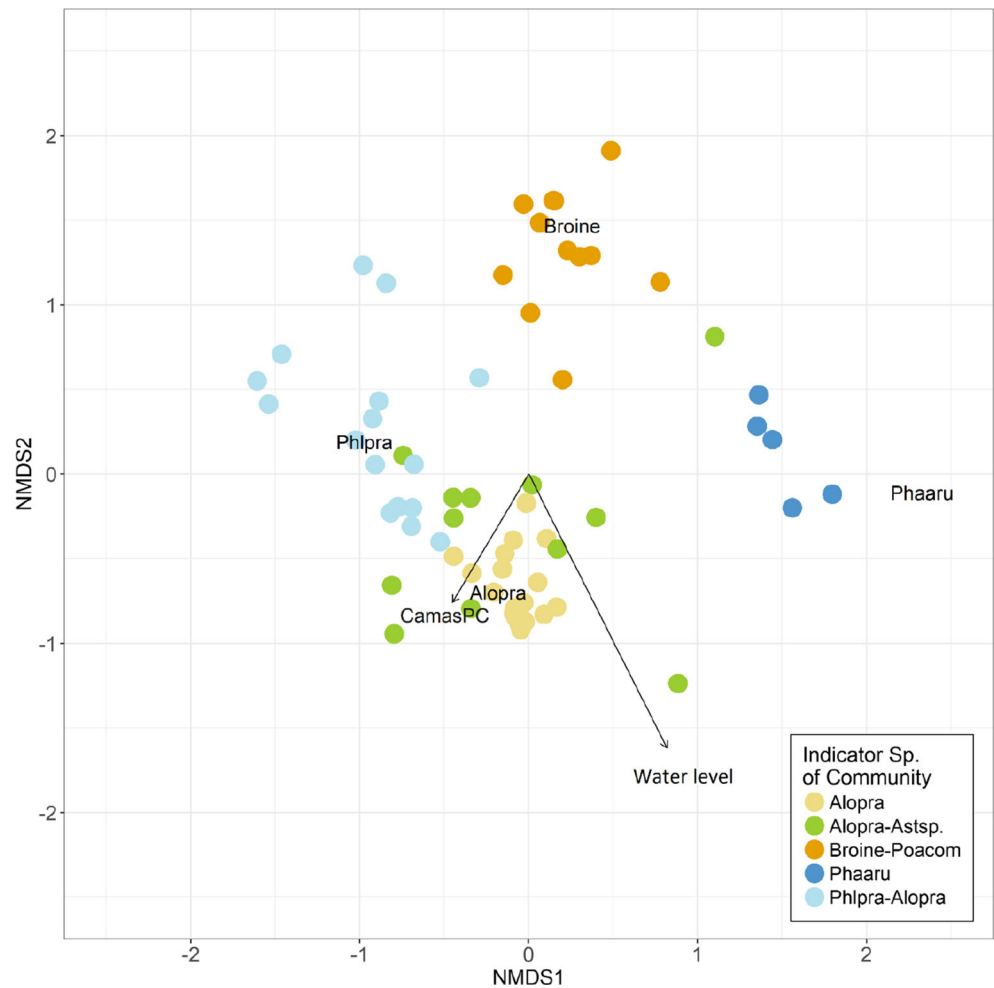


Fig. 13 Non-metric multidimensional scaling (NMDS) ordination of plots sampled in 2017. Colors indicate communities determined by flexible beta cluster analysis and classified by the species that contributed the greatest proportion of similarity within groups, as determined by SIMPER analysis. Water level is shown as a vector and was determined to be significantly correlated to projected plots. Presented species are dominant and show their distribution relative to communities (Broine = *Bromus inermis*, Phlpra = *Phleum pratense*, Alopra = *Alopecurus pratensis*, Junbuf = *Juncus bufonius*, Gnupal = *Gnaphalium palustre*, and Phaaru = *Phalaris arundinacea*)

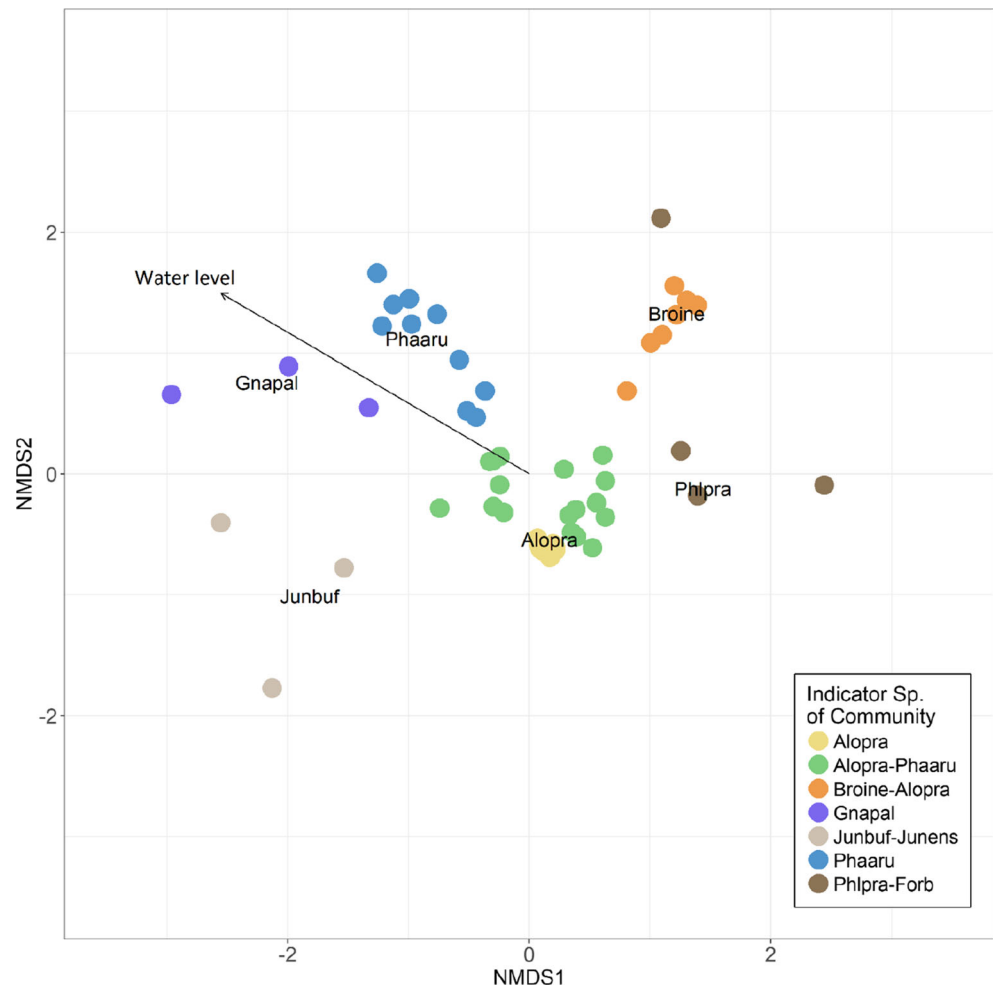


Fig. 14 Relative percent cover of planted (bottom, darker colors with stipples) and opportunistic (middle) species and bare ground (top) along cross-transsects on the filled ditch. Transect starts at the road culvert (0 m) and extends upstream to the property boundary at 280 m

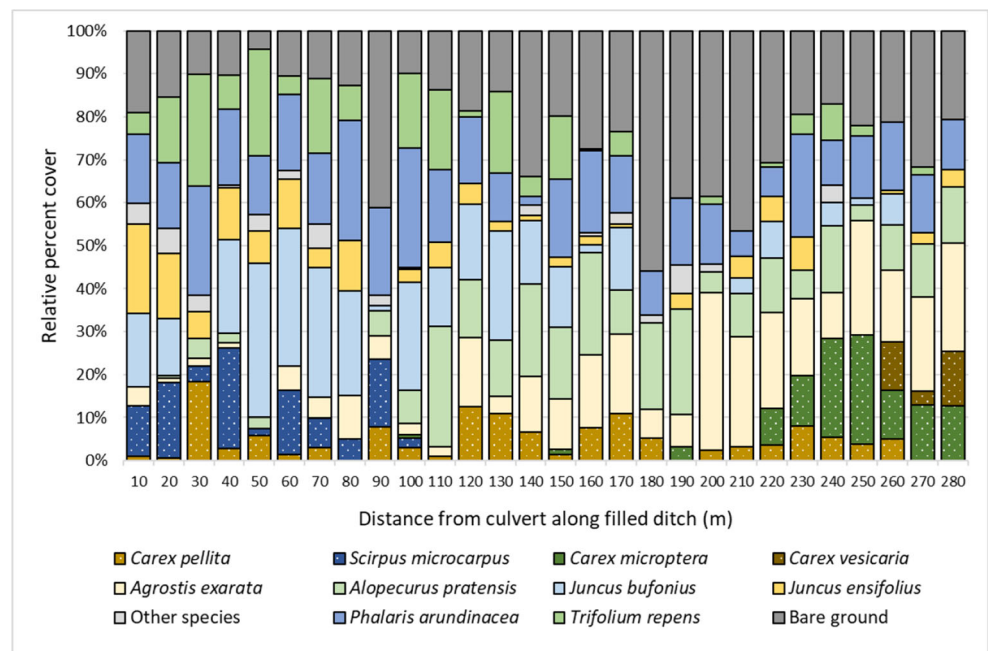


Table 3 Results from the Similarity Percentage analysis (SIMPER) of vegetation plots sampled in 2012 and 2017. The communities are grouped and named based in the species that contribute the highest

within-group average abundance. Results include average abundance, average similarity, similarity over standard deviation (Sim/SD), percent contribution (Contrib%), and cumulative contribution (Cum.%).

Year	Community name	Average similarity	Species	Average Abundance	Average Similarity	Sim/SD	Contrib%	Cum.%
2012	Alopra (<i>n</i> = 23)	82.93	<i>Alopecurus pratensis</i>	86.59	80.74	9.02	97.36	97.36
2012	Phlpra-Alopra (<i>n</i> = 16)	47.2	<i>Phleum pratense</i>	44.79	33.22	2.26	70.38	70.38
			<i>Alopecurus pratensis</i>	21.07	10.54	0.84	22.32	92.7
2012	Alopra-Astsp. (<i>n</i> = 12)	39.14	<i>Alopecurus pratensis</i>	36.03	27.49	2.09	70.25	70.25
			<i>Aster</i> species	13.75	2.99	0.31	7.65	77.9
			<i>Phleum pratense</i>	9.2	2.86	0.45	7.3	85.2
			<i>Agrostis gigantea</i>	10.5	2.81	0.42	7.19	92.39
2012	Broine-Poacom (<i>n</i> = 12)	56.41	<i>Bromus inermis</i>	53.03	43.07	3.73	76.35	76.35
			<i>Poa compressa</i>	20.68	9.45	0.75	16.75	93.1
2012	Phaaru (<i>n</i> = 8)	68.23	<i>Phalaris arundinacea</i>	79.32	66.15	3.14	96.96	96.96
2017	Phaaru (<i>n</i> = 10)	63.95	<i>Phalaris arundinacea</i>	70.17	58.55	3.83	91.56	91.56
2017	Alopra-Phaaru (<i>n</i> = 17)	60.07	<i>Alopecurus pratensis</i>	60.58	54.82	5.97	91.25	91.25
			<i>Phalaris arundinacea</i>	8.88	NA	NA	11.65	59.21
2017	Alopra (<i>n</i> = 27)	96	<i>Alopecurus pratensis</i>	96.99	95.41	36.52	99.39	99.39
2017	Gnapal (<i>n</i> = 3)	76.14	<i>Gnaphalium palustre</i>	80.18	70.08	106.8	92.04	92.04
2017	Junbuf-Junens (<i>n</i> = 3)	10.28	<i>Juncus bufonius</i>	28.72	6.58	1.13	63.96	63.96
			<i>Juncus ensifolius</i>	2.23	1.43	1.35	13.92	77.89
			<i>Gnaphalium palustre</i>	2.72	0.84	22.32	8.19	86.08
			<i>Eleocharis</i> species	4.85	0.55	0.58	5.32	91.39
2017	Broine-Alopra (<i>n</i> = 7)	74.4	<i>Bromus inermis</i>	72.88	65.88	7.13	88.55	88.55
			<i>Alopecurus pratensis</i>	7.04	3.82	1.63	5.14	93.69
2017	Phlpra-Forb (<i>n</i> = 4)	17.58	<i>Phleum pratense</i>	22.62	6.21	0.55	35.33	35.33
			Unk Forb	27.15	6.1	0.41	34.68	70.01
			<i>Alopecurus pratensis</i>	8.1	2.74	0.47	15.59	85.6
			<i>Bromus inermis</i>	5.96	1.41	0.41	8.03	93.64

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