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Water level drawdown induces a legacy effect on the seed bank and retains sediment chemistry in a eutrophic clay wetland

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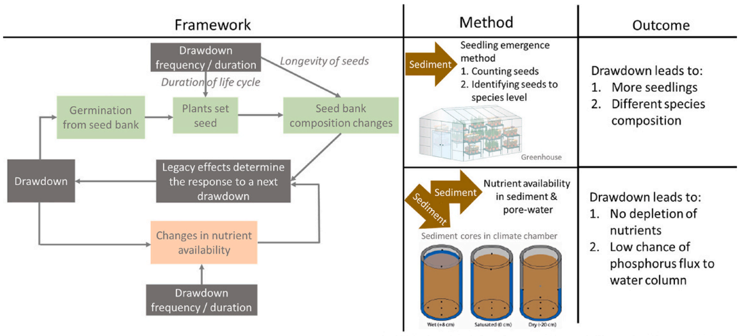
HIGHLIGHTS

- Inducing a drawdown in static eutrophic wetland systems can boost productivity.
- Drawdown history and higher elevations increase seed abundance in the seed bank.
- Water level fluctuations alter seed bank diversity although there is high variety.
- A multi-year drawdown alters seed bank species composition.
- An induced drawdown does not change nutrient availability in a eutrophic wetland.

GRAPHICAL ABSTRACT



Greenhouse pictogram: Tracey Saxby, Integration and Application Network (ian.umces.edu/media-library)

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ABSTRACT

The lack of extreme water level fluctuations in managed, non-peat forming wetland ecosystems can result in decreased productivity through the loss of heterogeneity of these ecosystems. Stochastic disruption, such as a water level drawdown, can effectively reverse this effect and return the wetland to a more productive state, associated with higher biodiversity through new vegetation development. Yet, aside from the effect on vegetation dynamics, little is known about longer-term effects (30 years) of a water level drawdown, hereafter referred to as legacy effects, and how this may impact future water level drawdowns.

Here, we aim to unravel the legacy effects of a water level drawdown, stand alone and along a water level gradient, on seed bank properties and nutrient availability in a eutrophic clay wetland. To identify these, we studied the hydrologically managed nature reserve Oostvaardersplassen in the Netherlands. Here, one section was subjected to a multi-year water level drawdown and another section was kept inundated. We determined

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seed bank properties in both areas, spatially and along a soil elevation gradient (20 cm). Nutrient availability was measured by taking sediment samples along the water level gradient and through experimental manipulation of the water level in an indoor mesocosm experiment.

Germination was higher in locations with a water level drawdown history, especially at relatively high elevations. Additionally, the proportion of pioneer species in the seed bank was higher in the water level drawdown area. Overall, nutrient concentrations were higher compared to other aquatic systems. Nutrient availability was higher in the inundated area and did not respond to the water level gradient. We conclude that 30 years after an induced water level drawdown there is no depletion of nutrients, while we still observe a legacy effect in the number of viable seeds in the seed bank.

1. Introduction

Hydrology is an important driving factor for wetland dynamics and functioning (Liu et al., 2020; Ma et al., 2010; Vulink and Van Eerden, 1998; Wilcox and Nichols, 2008). In non-peat forming wetlands, climatological variation determines whether vegetation succession is linear or cyclic by inducing selection through fluctuations in the water level (Van Geest et al., 2005). In natural wetlands there are several time scales on which these water level fluctuations (e.g., wet-dry cycles) can act. The smallest time scale is expressed in hours and entails for example wind-driven water movement that exposes sediment or floods small areas regularly (Hofmann et al., 2008). Seasonal water level fluctuations occur at a yearly timescale and are driven by seasonal variation in precipitation and evaporation (Johnson et al., 2010). Multi-year water level fluctuations are caused by events that occur every 20–30 years and are driven by extreme climate events, such as very dry summers or heavy precipitation (Johnson et al., 2010). Extremes that occur on a decadal time-scale are required to shift the system from an open-lake marsh towards a productive hemimarsh with both open water and surrounding emergent vegetation, such as *Phragmites australis* and *Typha* spp. (Carter Johnson et al., 2016; Farley et al., 2022; Johnson et al., 2010; Vulink and Van Eerden, 1998). With increasing anthropogenic pressure on wetland ecosystems, the natural extremes in water level fluctuations are dampened or non-existent due to a lack of connectivity and the construction of dams and dikes (Leyer, 2005; Tockner and Stanford, 2002). Long-term stability in water level can result in decreased productivity of wetland systems through the loss of heterogeneity (Mortsch, 1998; Johnson et al., 2010), which results in a climax vegetation state that is often associated with a lower biodiversity (Bakker et al., 2016; Farley et al., 2022; Johnson et al., 2010; Schummer et al., 2021; Wilcox, 2004).

The nature of the climax vegetation state, and the effects thereof on ecysystem functions, is wetland specific. For example, in peat forming wetlands, the climax vegetation may have higher heterogeneity (Benscoter and Vitt, 2008), while in non-peat forming wetlands (e.g., clay) the climax vegetation can have a low heterogeneity (Johnson et al., 2010; Mortsch, 1998). In this paper, we focus on non-peat forming and human-managed wetlands where productivity is thought to be enhanced by water level fluctuations due to increased heterogeneity in the landscape. In some human-managed wetlands, a multi-year drawdown is manually induced to mimic natural extremes and return the vegetation succession to a pioneer phase with high productivity (Farley et al., 2022; Odland and Del Moral, 2002; Raulings et al., 2011; Vulink and Van Eerden, 1998). Earlier research in these experimentally manipulated wetlands focused mostly on vegetation development (Farley et al., 2022; Odland and Del Moral, 2002; Raulings et al., 2011; Vulink and Van Eerden, 1998) or effects on wetland birds (Farley et al., 2022; Vulink and Van Eerden, 1998). Yet, a thorough understanding of how these induced water level drawdowns impact on the outcomes of successive water level drawdowns and whether the system continues to cycle in a similar fashion.

Such a 'landscape-scale water level drawdown' is applied in several wetlands around the world, including the human-made wetland Oostvaardersplassen in the Netherlands, (Vulink and Van Eerden, 1998), Myrkdalen lake in Norway (Odland and Del Moral, 2002), the brackish wetland Dowd Moras in South-Eastern Australia (Raulings et al., 2011) and the Montezuma wetland complex near New York, USA (Farley et al., 2022). Besides manipulating these hydrological conditions, set back of succession - or the steering thereof - was initiated by herbivory, such as in prairie glacial marshes through the water level and muskrat damage (*Ondatra zibethicus*) (Van Der Valk and Davis, 1978), through disease outbreaks or insect infestation (Tscharntke, 1999) and on the Marker-Wadden through grazing by herbivorous waterbirds (Temmink et al., 2022). Additionally, there is a need for these stochastic disruptions to reset vegetation succession not only in wetland systems but also in for example savannah ecosystems with the use of fire (Van Langevelde et al., 2003), in temperate forest landscapes, where succession from grassland to forest becomes cyclic in the presence of large herbivores (Olff et al., 1999), or in river ecosystems, where drifting ice resets vegetation succession (Lind et al., 2014; Lind and Nilsson, 2015; Prowse, 2001). These disruptions cause the main divergence from the well-known linear succession, in which a forest system is the most common climax state (van der Maarel, 1989), by allowing the system to return to an earlier successional stage and from there onwards linear succession continues. In wetlands a period of linear succession, characterized by little disruptions, leads to an alternative climax state where the system ends up in a lake-stage with just a perimeter of emergent vegetation (Liu et al., 2006, 2020; Murkin et al., 2000; van der Valk, 1981; Vulink and Van Eerden, 1998; Weller and Spatcher, 1965). A subsequent water level drawdown creates a window of opportunity for the remaining vegetation to restore from grazing pressure and for seeds to germinate on mudflats, which leads to rapid colonization of the area (Farley et al., 2022; Liu et al., 2006; Sarneel et al., 2014; Schummer et al., 2012). The plant community that is able to establish is a function of many interacting environmental filters, such as moisture content, nutrient availability, light conditions and timing and duration of a water level drawdown (Casanova and Brock, 2000; Sarneel et al., 2014; Ter Heerdt et al., 2017). The plant community at first predominantly consists of pioneer species, but will develop towards more perennial and emergent vegetation over time (Coops and Hosper, 2002; ter Heerdt, 2016). This development increasingly provides food and habitat for a wide array of species (Farley et al., 2022; Johnson et al., 2010; Liu et al., 2020; Schummer et al., 2012). Subsequent rewetting will favor the survival of water-tolerant species and, with the return of many herbivorous waterbound birds, the dense vegetation cover will become more heterogeneous, leading to increased habitat diversity (Vulink and Van Eerden, 1998). Finally, grazing by herbivores, during periods with a relatively stable water level, will increase the open-water area at the expense of vegetation cover, resulting in an open-water climax state (e.g., the circle is full) until a stochastic disturbance starts a new cycle (Murkin et al., 2000; Weller and Spatcher, 1965).

Whether such a this new cycle initiates a similar succession development can depend on legacy effects of the previous drawdown(s). Here, we define legacy effects as changes in an ecosystem that persist for a long time after the causal activity itself has ceased (adapted from Cuddington, 2011). Since changes during a water level drawdown could impact future wetland functioning through the depletion of the seedbank or nutrient availability, we will further discuss how these two variables might be altered during a water level drawdown in a eutrophic clay wetland (ter Heerdt, 2016; Vonk et al., 2017). The seed bank might be altered in a two-step manner. First, soil characteristics like soil moisture and soil elevation will determine which seeds from the present seed bank can germinate (Odland and Del Moral, 2002; Sarneel et al., 2014). Secondly, the species that eventually germinate will set seed and thereby replenish the seed bank (Capon and Brock, 2006; Van Der Valk and Davis, 1978). This in turn can potentially change the seed bank properties, like number of viable seeds, diversity and species composition, with each water level drawdown and thereby change the outcome of the following water level drawdown. Nutrient availability may be affected by a water level drawdown through the penetration of oxygen in the previously anaerobic sediment, which alters many biogeochemical processes in the soil, such as organic matter breakdown and phosphorus availability (Baldwin and Mitchell, 2000). Two of the macronutrients, nitrogen and phosphorus, are especially sensitive to soil oxygenation, which can lead to the loss of nitrogen from the sediment through the formation of nitrogen gas (Baldwin and Mitchell, 2000; Cavanaugh et al., 2006; James et al., 2004) and to the binding of available phosphorus to iron reducing its availability for plants (Lamers et al., 1997; Vonk et al., 2017). Consequently, without replenishment through the breakdown of organic matter or from external sources such as the inflow of nutrient-rich water, a water level drawdown may lead to a decline in nitrogen and phosphorus availability. This, in turn, could hinder the growth of vegetation in the subsequent water level drawdown phases.

The Oostvaardersplassen is a human-managed eutrophic clay wetland area in the province of Flevoland in the Netherlands. Flevoland was created after land reclamation in 1968 to fulfil a growing need for agricultural land (van Leeuwen et al., 2021). Part of Flevoland remained wet and since the agricultural requirements of the land reclamation were met, the area remained undeveloped and was left for spontaneous nature development now known as Oostvaardersplassen (Cornelissen et al., 2014; Jans and Drost, 1995). The 3600 ha large marshland part of the nature reserve (5600 ha) lacked high-amplitude, multi-year water level dynamics due to the construction of dikes, weirs and, the lack of connectivity with lakes and rivers. This resulted in an open-water marsh state associated with a strong decline in bird numbers and diversity in the area, circa 15 years after creation. To restore bird habitat, specifically reed vegetation (*Phragmites australis*), by resetting the successional stage, nature managers decided to artificially induce a water level drawdown in part of the area from 1987 till 1991. This has been done by installing a weir to let the water out during high water level or with the right wind direction. The water that remains due to the height of the weir will evaporate over the summer to complete the drawdown process. This also means that, in periods with a lot of rainfall (e.g., over the winter), the area will become inundated again with a layer of water. However, it remains unknown what the long-term effect, in this case after 30 years, of a water level drawdown, hereafter referred to as legacy effects, are and how they interact with small seasonal fluctuations along a water level gradient. Additionally, the question rises whether this measure is reproducible or whether repetition will on the long-term hamper ecosystem functioning through nutrient depletion or lack of viable seeds (James et al., 2007; Vonk et al., 2017). To assess the repeatability of such a measure on the longer term, it is necessary to understand whether there are any long-term legacy effects on nutrient availability, the pathway of vegetation succession and on wetland functioning.

In this paper, we aim to unravel the legacy effects of a water level drawdown on seed bank properties and nutrient availability, and its interaction with a water level gradient caused by elevational differences (+/− 20 cm) in a eutrophic clay wetland. We selected the nature reserve Oostvaardersplassen in the Netherlands based on its two distinct hydrological regimes, one with a multi-year water level drawdown from 1987 till 1991 and one without intervention remaining relatively stable over time since reclamation. We applied a mixed-method approach by conducting field surveys coupled to a mesocosm experiment. To determine legacy effects of a previously induced water level drawdown on germination and nutrient availability and to assess these variables along an elevational gradient, we collected soil samples in the field for later germination in the greenhouse or analysis in the lab respectively. To determine the impact of water level (inundated, saturated, dry) on nutrient availability and germination we conducted an eight week indoor mesocosm-experiment using intact sediment cores from Oostvaardersplassen. We hypothesized that a historical water level drawdown and an increase along a water level gradient lead to (1) a higher seed abundance in the seed bank, (2) a greater seed diversity in the seed bank, (3) alterations in species composition compared to the non-water level drawdown area, probably skewed towards more pioneer species in the water level drawdown area instead of towards perennial species that are currently growing in both areas, like *Phragmites australis*, *Typha* spp. and *Salix* spp., and (4) changes in nutrient availability, specifically a decrease in nitrogen and phosphorus.

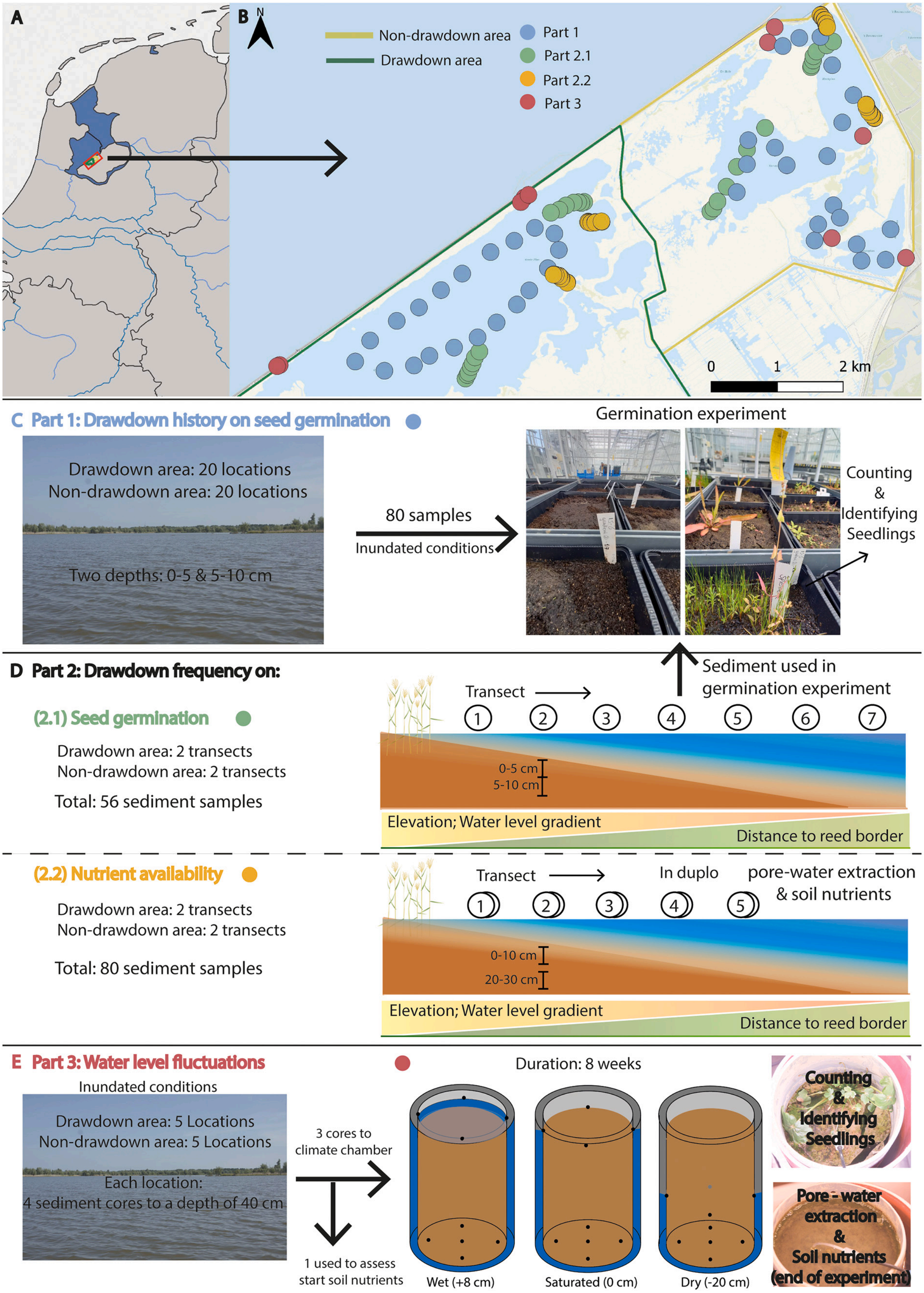
2. Materials and methods

2.1. Study site

The study was conducted in Oostvaardersplassen in the Netherlands (coordinates: 52.456857, 5.355935). This eutrophic clay wetland of about 5600 ha consists of a 3600 ha marsh and a 2000 ha dryer border zone. This study took place in the marsh part (Fig. 1A–B). The marsh is characterized by large water bodies, reed vegetation and willow forests. Oostvaardersplassen is part of the polder Zuidelijk Flevoland, which is located in the former Zuiderzee estuary, a marine habitat (see van Leeuwen et al., 2021 for a detailed description). For water safety reasons, the decision was made to separate the inland Zuiderzee from the North Sea through the construction of a dike, named the Afsluitdijk. After completion of the construction and within five years, the Zuiderzee transformed into a freshwater lake, IJsselmeer. In this freshwater lake, several polders were established to create land for agriculture; Zuidelijk Flevoland was reclaimed in 1968. Since Oostvaardersplassen is located in, what was then, the lowest part of the polder, it remained wet during the first years after reclamation and no actions were taken to develop this area into the industrial site as it was planned to be (Cornelissen et al., 2014).

The marine clay soil and its associated high nutrient concentrations (eutrophic) in combination with the unmanaged and wet conditions, led nature to develop quickly. This made the area into an important breeding and resting area for many wetland birds and therefore became a protected wetland nature reserve in 1974. In 1989 it became a protected area within the European Bird directive and under the Ramsar agreement. Additionally, it was qualified as a Natura 2000 area in 2009. Later on, the relatively high water levels at the end of winter, due to the height of the weir, in combination with high grazing pressure by moulting greylag geese (*Anser anser*) from May to July, resulted in the loss of reed cover (*Phragmites australis*) (Vulink and Van Eerden, 1998). This in turn resulted in decreasing bird numbers due to lower food and habitat availability (Beemster et al., 2010). To restore reed-dominated wetlands and to increase food and habitat availability for birds, a complete multi-year water level drawdown was induced in the western part of the marsh from 1987 till 1991 (Figs. 1 and S1) (Vulink and Van Eerden, 1998). The eastern part was hydrologically separated from the western part by a low dike (Figs. 1B and S1) and water levels and dynamics remained unchanged in this area. The implemented water level drawdown resulted in the development of c. 600 ha of reed-dominated vegetation in the western part, after which typical wetland birds, e.g., bearded reedling (*Paranrus biarmicus*), marsh harrier (*Circus aeruginosus*) and Eurasian bittern (*Botaurus stellaris*), increased in numbers (Beemster et al., 2012; Vulink and Van Eerden, 1998).

The study area experiences seasonal variation in water level, but lacks long-term dynamics in water level that would be caused by extreme climatological periods. As the marsh is rainwater fed, natural water level dynamics occur with a high water level at the end of winter



(caption on next page)

Fig. 1. (A) Location of the study area (the Oostvaardersplassen) in the Netherlands indicated by the black dot. (B) Overview of the Oostvaardersplassen and its division in non-water level drawdown area and water level drawdown area, shown by the yellow and green delineation respectively. Dots indicate sampling points and its color indicates the used method (C, D & E). (C) Method for determining the effect of water level drawdown history on seed germination by sampling 20 locations ($n = 20$, blue dots in B) in both the water level drawdown area and the non-water level drawdown area at depths of 0–5 and 5–10 cm. After collection samples were kept at -8 °C for one month to allow seed stratification. Subsequently, sieved samples containing the seeds were held in the greenhouse for a period of 5 months to allow seedlings to germinate. (D) Method for assessing the effect of water level drawdown frequency on seed germination and nutrient availability. (1) Two transects each consisting of 7 sampling points were sampled in both the water level drawdown area and the non-water level drawdown area ($n = 14$, green dots) at depths of 0–5 and 5–10 cm. Further method for assessing seed germination is the same as described at C. (2) Two transects each consisting of 5 sampling points that were sampled in duplicate in both the water level drawdown and the non-water level drawdown area ($n = 10$, yellow dots) at depths of 0–10 cm and 20–30 cm. Afterwards, pore-water was extracted from the sediment samples for nutrient analysis and fresh soil was dried and ashed to determine water content and organic matter content. Using the fresh and the dried soil, salt and p-olsen extractions were performed respectively. (E) Intact sediment cores were collected from the field site and kept in a climate chamber under stable conditions to assess the effect of water level and water level drawdown history on seed germination and nutrient availability.

(March) and low levels at the end of summer (September; Fig. S1). The surplus of water in winter leaves the marsh via a weir. The average difference in water level between summer and winter is approximately 30 cm. During 'dry' summers the water level can drop 50 cm at the end of the growing season. Due to both the climate conditions in combination with the height of the weir, set as to pertain high water levels in the reed beds during late winter and spring, these naturally occurring 'dry' summers did not result in enough mudflat exposure throughout the area to allow extensive marsh recovery. At the time of sampling, both the water level drawdown and the non-water level drawdown area were characterized by a sharp border between vegetation and open water. The vegetation on the shores was similar in both areas and dominated by *Phragmites australis*, *Salix* spp. and, to a lesser extent, *Convolvulus* spp. At drier sites, with greater proximity to the lake, *Urtica dioica* and *Carduus* spp. were present in higher abundances. The shores of the lake, that sometimes fall dry during dry summers, are colonized quickly by species among which *Tephroseris palustris* (also known as *Senecio congestus*), *Epilobium hirsutum* and *Ranunculus sceleratus*. For more information on the present species we refer to Fig. S2.

2.2. *Experimental design*

We examined the legacy effects of a water level drawdown, a water level gradient and water level fluctuations on seed bank germination and nutrient availability using field sampling and mesocosm experiment (Fig. 1C–E). The unique field situation consisting of areas with and without a water level drawdown history allows to explore legacy effects on seed bank properties (Part 1.1) and nutrient availability (Part 2.1). This approach focusses on the long-term effects of inducing a four-year water level drawdown, in this case 30 years after the event, by sampling 20 locations in each subarea that have been inundated since the last water level drawdown. In addition, soil samples have been taken in these two hydrologically distinct areas, along a water level gradient that is dictated by elevational differences of about 20 cm. With this approach, we used the elevational gradient to distinguish between higher locations, that would fall dry more often due to for example dry summers, and lower locations. The latter had not fallen dry for 30 years in case of the water level drawdown area and 50 years in case of the non–water level drawdown area. By taking soil samples on 7 (germination) or 5 (nutrient) locations along this water level gradient, we were able to research how changes in water level alter seed bank properties (Part 2.1) and nutrient availability (Part 2.2) on a smaller seasonal time scale. In addition to the above two sampling campaigns, a mesocosm experiment was conducted to study the effects of water level on germination (Part 3.1) and nutrient availability (Part 3.2) . With this approach it was possible to determine effects of a specified water level (inundated, saturated, dry) on an even smaller time scale of weeks/ months and how such a response might be influenced by events in the past, in this case drawdown history.

2.2.1. *Part 1: water level drawdown history*

To investigate the legacy effects of a previously induced water level drawdown on the seed bank (part 1.1) and on nutrient availability (part 1.2), we compared seed bank properties (density, diversity, species composition; Fig. 1C) and sediment nutrient concentrations between an area with water level drawdown history and an area without. For the method on sediment nutrient concentrations we would like to refer to the section on water level gradient (Section 2.2.2) for field sampling and lab protocols.

2.2.1.1. Seed bank properties (part 1.1). We collected sediment samples from both areas in Oostvaardersplassen in June 2021, when both areas were still inundated. To cover the spatial heterogeneity of the area, 40 locations were sampled (Fig. 1, blue dots). 20 Sample points were located in the area that was continuously inundated for 50 years (non-water level drawdown history, $n = 20$) and 20 in the area that had undergone a water level drawdown from 1987 till 1991 and was subsequently inundated for 30 years (water level drawdown history, $n = 20$).

In June 2021, we took ten sediment cores of 23.8 cm^2 (diameter = 5.5 cm) to a depth of 10 cm and pooled the 0–5 cm and 5–10 cm depth in separate plastic bags at each location (Verhofstad et al., 2017). The bags were stored in the dark at 4 °C for approximately one month to allow seed stratification, after which the sediment was sieved (mesh width: 150 μm) and the residue, containing the seeds, was spread across a tray (37 × 27 cm) containing sediment for propagation and germination (Lensli substrates; pH = ~5.3; electrical conductivity = ~0.5mS/cm). The trays were placed in a greenhouse with supplementary light from 6:00–22:00 h so that light conditions on plant level corresponded with 250 μmol.m^2/s. The temperature in the greenhouse was on average 21 °C between 6:00–22:00 and 16 °C between 22:00–6:00. The relative humidity (Rh) in the greenhouse was on average 60 % (−5/+5 %). To ensure optimal sediment moisture, the trays were watered at least once a week with rainwater. The germinating plants were then identified to species level and removed afterwards. This was done to minimize possible competition effects between seedlings. Unidentified plants were transferred from the trays to individual pots, providing the space for them to grow and/or flower until their identification could be determined. When germination stopped, the sediment was mixed to allow seeds deeper in the sediment to germinate. The trays were kept in the greenhouse until germination stopped again, which lasted up to 5 months.

2.2.2. *Part 2: water level gradient*

To determine how a water level gradient, induced through a gradient in soil elevation of around 20 cm, affects seed bank properties (density, diversity, species composition; Part 2.1) and nutrient availability (part 2.2), we collected sediment samples in the field (Fig. 1B,D). Sample collection occurred at seven locations (seed bank) and five locations (nutrient availability) along four transects perpendicular to the border of the reed vegetation. The indicated direction was chosen to cover differences in soil elevation, with locations on a relatively higher elevation falling dry more often due to small fluctuations in the water level and locations on a lower elevation falling dry less often (Fig. S3).

2.2.2.1. Seed bank properties (part 2.1). To assess how a water level gradient alters seed bank properties, we collected sediment samples in June 2021 along four transects, each consisting of seven sampling points ($n = 28$; Fig. 1D). The sampling points cover a gradient of soil elevation, where the locations indicated by a 1 are located at the highest elevation, and thus fall dry the most, while locations indicated by a higher number (2–7) are decreasing in soil elevation and thus fall dry less often or never. Each transect covered around 777.5 ± 418.7 m. Two transects were located in the area without water level drawdown history and two in the area with water level drawdown history (Figs. 1B, S1 and S3). The sampling and germination protocol was identical to the one described in Section 2.2.1.

2.2.2.2. Nutrient availability (part 2.2). To examine how a water level gradient affect nutrient availability, sediment samples were collected along four transects (different from the transects in Section 2.2.2.1, see Fig. 1B) in November 2021. Each transect consists of five sampling points that were sampled in duplicate ($n = 40$; Figs. 1D and S3). The sampling points cover a gradient of soil elevation, where the locations indicated by a 1 are located at the highest elevation, and thus fall dry the most, while locations indicated by a higher number (2–5) are decreasing in soil elevation and thus fall dry less often or never. Each transect covered around 237.5 ± 17.9 m. Two transects were situated in the area without water level drawdown history and two in the area with water level drawdown history (Fig. 1B). At each sampling location, four sediment cores of 23.8 cm^2 (diameter = 5.5 cm) to a depth of 0–10 cm and 20–30 cm were collected for pore-water extraction and one sediment core of 23.8 cm^2 (diameter = 5.5 cm) to a depth of 0–10 and 20–30 cm was collected for sediment nutrient analyses. Soil elevation measurements were conducted with a dGPS (Topcon, HiPer SR). At each location, we took three measurements which were averaged.

Pore-water extraction was initiated in the lab on the same day as sediment collection and collected the next morning. Pore-water samples were extracted using vacuum syringes attached to rhizons (Rhizon SMS; Rhizosphere Research Products; Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands). The pore-water was analyzed for pH, alkalinity (Metrohm, 877 Titrino plus) (Fig. S4), total inorganic carbon (TIC; infrared carbon Analyser, IRGA; ABB Analytical, Frankfurt, Germany) and nutrient concentrations (Tables S1 and S2, supplementary material S1).

Sediment samples were analyzed on water content, bulk density loss of ignition (LOI; proxy for organic matter content) and bioavailable phosphorus and NH_4^+ and NO_3^-. The elaborated method can be found in the supplementary material S1. Nitrite (NO_2^-) concentrations were barely detectable and therefore left out of the analysis.

2.2.3. Part 3: water level fluctuations

2.2.3.1. Experimental setup. To unravel how water level influences germination (part 3.1) and nutrient availability (part 3.2), we performed a mesocosm experiment with different water levels on intact sediment cores from sites with and without water level drawdown history from Oostvaardersplassen (Fig. 1D). The different water levels reflect the different stages the system goes through during the first phase (drying) of a water level drawdown cycle: (1) Dry, the water level was 20 cm below sediment surface level ('dry' for brevity), (2) saturated, the water level was equal to the sediment surface level ('saturated' for brevity), and (3) wet, the water level was eight cm above sediment surface level ('wet' for brevity, Fig. S5). The experiment ran for eight consecutive weeks in which each core experienced one of the water level treatments (inundated, saturated or dry) following Vonk et al. (2017). In November 2020, intact sediment cores were collected from Oostvaardersplassen at ten locations that were inundated. Half of these locations were situated in an area with a water level drawdown history ($n = 5$, water level = 13.8 +/− 3.9 cm), while the other half were situated in a continuously inundated area ($n = 5$, water level = 17 +/− 5.4 cm). At each location, four sediment cores with a diameter of 16 cm and a depth of 40 cm were collected by pressing a PVC-tube in the sediment and sealing it with a cap on the bottom. Three of the intact cores for each location were placed in a climate room for an acclimation period of six days, after which the experiment started. The cores were placed in the climate room with a temperature regime of 20 °C from 6:00–22:00 and 15 °C from 22:00–6:00. The average humidity in the climate chamber was 45 % and the average light conditions at sediment level were 554 μmol.m^2/s (LI-COR LI-250 photometer) with 16 h light and 8 h dark. The cores were placed using a randomized block design ($n = 5$), each block consisted of six sediment cores (Table S3). The treatments were applied by drilling holes in the PVC-tube at the corresponding water level treatment height (−20 cm, 0 cm, +8 cm relative to the sediment height). To regulate the water level in the core, we placed the PVC-tube in a larger water-proof PVC-core (diameter = 20 cm, length = 50 cm; Fig. S5). Water collected from the Oostvaardersplassen was used to initiate the treatments. During the experiment, water was replenished till treatment level with rainwater (pH = 5.18, alkalinity = 0.33 mEQ/L). The fourth core was used to determine sediment nutrient starting conditions by taking two sediment samples of 40 cm deep (23.8 cm^2) after which it was split in two sections of 10 cm (0−10,20−30). The two sediment samples from the sediment core were pooled per location and per depth and stored in the freezer at −20 °C until further analyses. The same analysis protocol was used as in approach 2 (Section 2.2.2.2).

2.2.3.2. Seed bank properties(part 3.1). Through the use of intact soil cores in an experimental setup, we could identify possible environmental filters that would exert selection on the type of plants that were able to germinate during different phases of a water level drawdown cycle. During the 8-week experiment, the mesocosms were checked weekly for plant germination. Germinated plants were counted and identified to species level if possible. Plants were not removed during the experiment.

2.2.3.3. Nutrient availability (part 3.2). The experimental setup allowed us to assess how a certain water level regime impacts nutrient availability in the system, in this case, we selected three water levels to mimic different phases of the water level drawdown cycle. By monitoring these changes it would be possible to identify possible nutrient depletion in the system upon repeated water level drawdown implementation. Nutrient concentrations were determined in both the pore-water and the sediment. To collect pore-water samples during the experiment, rhizons (Rhizon SMS; Rhizosphere Research Products; Eijkelkamp Agrisearch Equipment, Giesbeek, The Netherlands) were installed in the sediment core at a depth of 10 cm and a vacuum syringe could be attached to extract pore-water. This was done at the start of the experiment (day 0), and repeated five times on day 7, 14, 21, 35 and 56. Pore-water samples were analyzed in the same way as in approach 2. At the end of the experiment, sediment samples were taken from the sediment cores at two different depths (0–10 cm and 20–30 cm) following the same sampling strategy as at the start of the experiment. These samples were stored in the freezer at −20 °C until further analyses, following the analysis protocol as described in approach 2 (Section 2.2.2.2).

2.3. Statistical analyses

Data were analyzed in RStudio version 4.0.3 (R Core Team, 2023). For all hypotheses testing procedures the significance level was set at $\alpha = 0.05$. All data are shown with their average ± standard deviation (sd).

2.3.1. Part 1: water level drawdown history

2.3.1.1. Part 1.1 seed bank properties. To determine the effect of water level drawdown history (Yes or No) on mean Shannon-Wiener diversity, mean species richness, and mean germination densities (log transformed), we used mixed linear models from the GlmmTMB package (Mollie et al., 2017), using location ID as a random effect. Differences in the total sum of germinated individuals between the water level drawdown and non-water level drawdown area were tested using a Chi-Square test. Shannon-Wiener diversity was calculated using the 'vegan package' (Oksanen et al., 2022). To assess the effect of water level drawdown history on species composition a permanova analysis with a Bray-Curtis dissimilarity index was used, in combination with non-metric multidimensional scaling (NMDS) (vegan package: Oksanen et al., 2022).

2.3.1.2. Part 1.2 nutrient availability. To determine the effect of water level drawdown history and sampling depth (independent variables) on the nutrient availability (dependent variables) along the transect survey (method Section 2.2.2.2), we used mixed linear models from the GlmmTMB package (Mollie et al., 2017). The model was performed for both the sediment- and the pore-water nutrient concentrations. Location ID was used as a random effect to correct for the duplicate measurements. Tukey-adjusted comparisons were done using "emmeans" (Russell, 2022). Normality and heterogeneity of the residuals of the models were assessed using histograms, and transformed if necessary (Tables S1 and S4).

Additionally, we used the nutrient starting concentrations from the experimental water level experiment (part 3) to determine differences in nutrient concentrations due to the water level drawdown history. To determine the effect of water level drawdown history (independent variable) on nutrient availability (dependent variables), we used mixed linear models from the GlmmTMB package (Mollie et al., 2017). Starting nutrient concentrations (day 0; field conditions) were used as the dependent variable. Field location ID was used as a random effect to correct for samples taken at the same location.

2.3.2. Part 2: water level gradient

2.3.2.1. Part 2.1 seed bank properties. To determine the best fit of the relation between germination and distance to the reed border, we compared the AIC of linear, parabolic, hyperbolic and exponential decay functions. An $\Delta AIC \geq 2$ was used to differentiate models ('stats' package (R Core Team, 2023). To assess the effect of water level drawdown history and location along soil elevation gradient on species composition, a permanova analysis with a Bray-Curtis dissimilarity index was used in combination with non-metric multidimensional scaling (NMDS) (Oksanen et al., 2022).

To determine differences in Shannon-Wiener diversity, species richness and germination densities (dependent variables) along the transect survey (location within transect as independent variable), we used mixed linear models from the GlmmTMB package with location ID as a random effect (Mollie et al., 2017). Species richness was fitted with a Poisson distribution. This approach was done separately for the water level drawdown and the non-water level drawdown area. Tukey-adjusted comparisons were done using "emmeans" (Russell, 2022). Shannon-Wiener diversity was calculated using the 'vegan package' (Oksanen et al., 2022). Differences in the sum of germinated individuals per location along the water level gradient were tested using a Chi-Square test.

2.3.3. Part 2.2 nutrient availability

To test for differences in nutrient availability along the elevational gradient of current water level fluctuations in the transect survey, we performed Spearman correlations (Tables S2 and S5). The Spearman correlations were done between nutrient concentration as the dependent variable and elevation in meters NAP as the independent variable.

2.3.4. Part 3: water level fluctuations

2.3.4.1. Part 3.1: seed bank properties. Due to the low germination rate, no statistical analysis were performed on seed bank properties in relation to any of the water level treatments.

2.3.4.2. Part 3.2: nutrient availability. To determine the effect of water level treatment (independent variable) on nutrient availability (dependent variables), we used mixed linear models from the GlmmTMB package (Mollie et al., 2017). Nutrient concentrations from the end of the experiment (day 56) were used as dependent variable. Nutrient starting concentrations were used as a covariate into the model and the blocking factor was used as a random effect. Additionally, nutrient concentrations were tested for changes over time during the eight-week experiment using mixed linear models from the GlmmTMB package (Mollie et al., 2017). Nutrient concentrations were used as the dependent variable, the blocking factor was used as a covariate in the model and date was used as the independent variable. To test for differences among the independent variables, Tukey-adjusted comparisons were done using "emmeans" for all models (Russell, 2022). All models were fitted with a Gaussian-error distribution. Normality and heterogeneity of the residuals of the models were assessed using histograms, and were transformed if necessary (Tables S6, S7, S8, S9 and Fig. S6).

3. Results

3.1. Part 1: water level drawdown history

3.1.1. Part 1.1 seed germination

In total 842 individuals of 26 different species germinated from the sediment collected at 40 locations in both the water level drawdown and non-water level drawdown area (Table S10). Germination was not affected by depth (Table S11). The total amount of germinated plants was higher in the area with water level drawdown history (517) than in the area without water level drawdown history (325) ($X^2 = 43.78$, $p < 0.01$). Mean germination, seed density and species richness did not differ between the area with water level drawdown history and the area without water level drawdown history (respectively: $t = -1.02$, $p = 0.31$; $X^2 = 0.38$, $p = 0.54$; $X^2 = 1.50$, $p = 0.23$) (Table 1). Species diversity was found overall higher in the area without water level drawdown history compared to the area with water level drawdown history ($X^2 = 4.10$, $p = 0.04$; Table 1). The permanova analysis showed a significant effect of water level drawdown history on species composition ($p = 0.001$; Fig. 2). The area with water level drawdown history is characterized by pioneer species as *Epilobium hirsutum*, *Persicaria* spp., *Rumex maritimus*, *Lycopus europaeus* and *Atriplex prostrata*. The area without water level drawdown history is characterized by more perennial species, such as *Typha latifolia* and *Phragmites australis* and some pioneer species growing in wet habitats, such as *Chenopodium rubrum*, *Veronica anagallis-aquatica* and *Rorippa palustris*.

3.1.2. Part 1.2 nutrient availability

3.1.2.1. Field sampling. Soil ammonium concentrations were highly variable, and lower in the area with water level drawdown history (1560 ± 1600 μmol/L FW) compared to the area without water level drawdown history (3470 ± 2900 μmol/L FW; Table S4). Soil phosphorus and nitrate concentrations did not differ (Table S4), while potassium was almost a factor 2 lower in the water level drawdown area (7650 ± 2900 μmol/L/FW) compared to the non-water level drawdown area (12,300 ± 6000 μmol/L/FW). In addition, porewater phosphorus concentration was a factor 10 lower in the water level drawdown area, while porewater calcium, magnesium, potassium, sodium, sulfur and Fe:P ratio were higher in the water level drawdown area compared to the non-water level drawdown area (Table S1).

Table 1
Mean and standard deviation for the number of individuals that germinated, the diversity index, species richness and seed densities for the area without water level drawdown history (No) and the area with water level drawdown history (Yes) for both the sampling on water level drawdown history (30 years after water level drawdown) and on locations along a water level gradient. The sampling points were lying on a gradient of soil elevation, where the locations indicated by a 1 are located at the highest elevation, and thus fall dry most often, while locations indicated by a higher number (2–5) are decreasing in soil elevation, and thus fall dry less often or never. The letters in the column "30 years after drawdown" show if there are statistical differences in each of the variables for the independent variable "drawdown history" (no differences were found). The letters in the columns for the locations 1 to 7 show for each variable and the two levels of drawdown history (8 rows) whether there is a statistical difference along the water level gradient (mean is based on the sampling of two transects).

			30 years after drawdown	Water level gradient 1	Water level gradient 2	Water level gradient 3	Water level gradient 4	Water level gradient 5	Water level gradient 6	Water level gradient 7
Variable	Unit	Drawdown history	Mean ± sd	Mean ± sd	Mean ± sd	Mean ± sd	Mean ± sd	Mean ± sd	Mean ± sd	Mean ± sd
Germination	#, nr of individuals	No	8.1 ± 8.2 (a)	671.8 ± 224.6 (ab)	629.25 ± 417.60 (ab)	995.5 ± 1162.0 (b)	612.3 ± 849.5 (ab)	5.3 ± 2.8 (a)	5.8 ± 5.4 (a)	5.8 ± 8.3 (a)
		Yes	12.9 ± 25.7 (a)	14.5 ± 11.3 (ab)	14.25 ± 5.32 (ab)	9.8 ± 3.6 (ab)	7.5 ± 5.1 (ab)	4.8 ± 3.1 (ab)	16.0 ± 12.0 (a)	1.3 ± 0.1 (b)
Diversity	Exp(Shanon-Wiener index)	No	2.4 ± 1.4 (a)	3.5 ± 1.7 (a)	4.78 ± 3.22 (a)	1.8 ± 0.8 (a)	1.5 ± 0.5 (a)	2.0 ± 1.1 (a)	2.3 ± 1.3 (a)	2.6 ± 2.0 (a)
		Yes	2.0 ± 0.8 (b)	4.9 ± 2.0 (a)	3.61 ± 0.82 (ab)	3.8 ± 1.3 (ab)	3.4 ± 2.8 (ab)	2.0 ± 0.8 (ab)	3.1 ± 1.4 (ab)	1.3 ± 0.5 (b)
Species richness	#, nr of species	No	2.4 ± 1.4 (a)	14.0 ± 4.1 (a)	15.8 ± 1.5 (a)	5.5 ± 3.5 (b)	6.3 ± 5.6 (b)	2.3 ± 1.3 (b)	2.5 ± 2.1 (b)	2.5 ± 2.7 (b)
		Yes	2.0 ± 1.2 (a)	6.0 ± 2.5 (a)	4.75 ± 1.26 (ab)	4.3 ± 1.5 (ab)	3.8 ± 3.5 (ab)	2.3 ± 1.0 (ab)	3.8 ± 1.0 (ab)	1.3 ± 0.5 (b)
Seed densities	Seeds/m^2	No	6.3 ± 6.1 (a)	28.3 ± 8.9 (a)	26.50 ± 19.8 (a)	41.9 ± 59.0 (a)	25.8 ± 36.4 (a)	0.2 ± 0.1 (a)	0.2 ± 0.2 (a)	0.2 ± 0.3 (a)
		Yes	9.0 ± 13.4 (a)	0.6 ± 0.4 (ab)	0.60 ± 0.07 (ab)	0.4 ± 0.1 (ab)	0.3 ± 0.1 (ab)	0.2 ± 0.1 (ab)	0.7 ± 0.2 (a)	0.1 ± 0.1 (b)

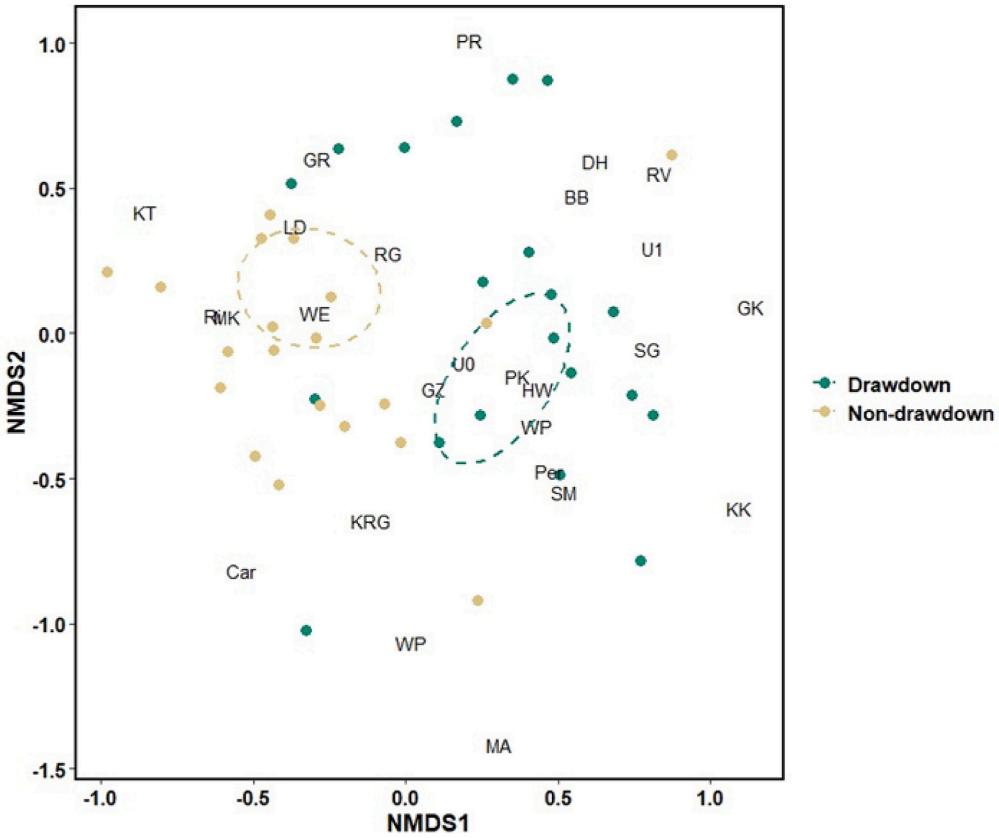


Fig. 2. Non-metric multidimensional scaling plot (stress = 0.18, dimensions = 3, Bray-Curtis dissimilarity) for germinated plants in the area with artificial water level drawdown history and the area without water level drawdown history ($n = 20$). Dotted lines represent the centroids of the two groups and visualize the overlap in species composition. The acronyms in the figure indicate different plant species. An overview of the plant species described by each acronym can be found in the additional information (Table S10). Permanova analysis showed a significant effect of water level drawdown history ($p = 0.001$).

3.1.2.2. Experimental setup. At the start of the experiment (i.e., site conditions), pore-water phosphorus concentrations were similar across water level drawdown history ($p = 0.5$; Figs. 3, S7). Like in the field samples, the Fe:P ratio in the area with water level drawdown history is higher (3.67 ± 2.53) than in the non-water level drawdown area (2.78 ± 4.42; $p = 0.05$). Similarly, both sodium and chloride are *c.* 1.5 times

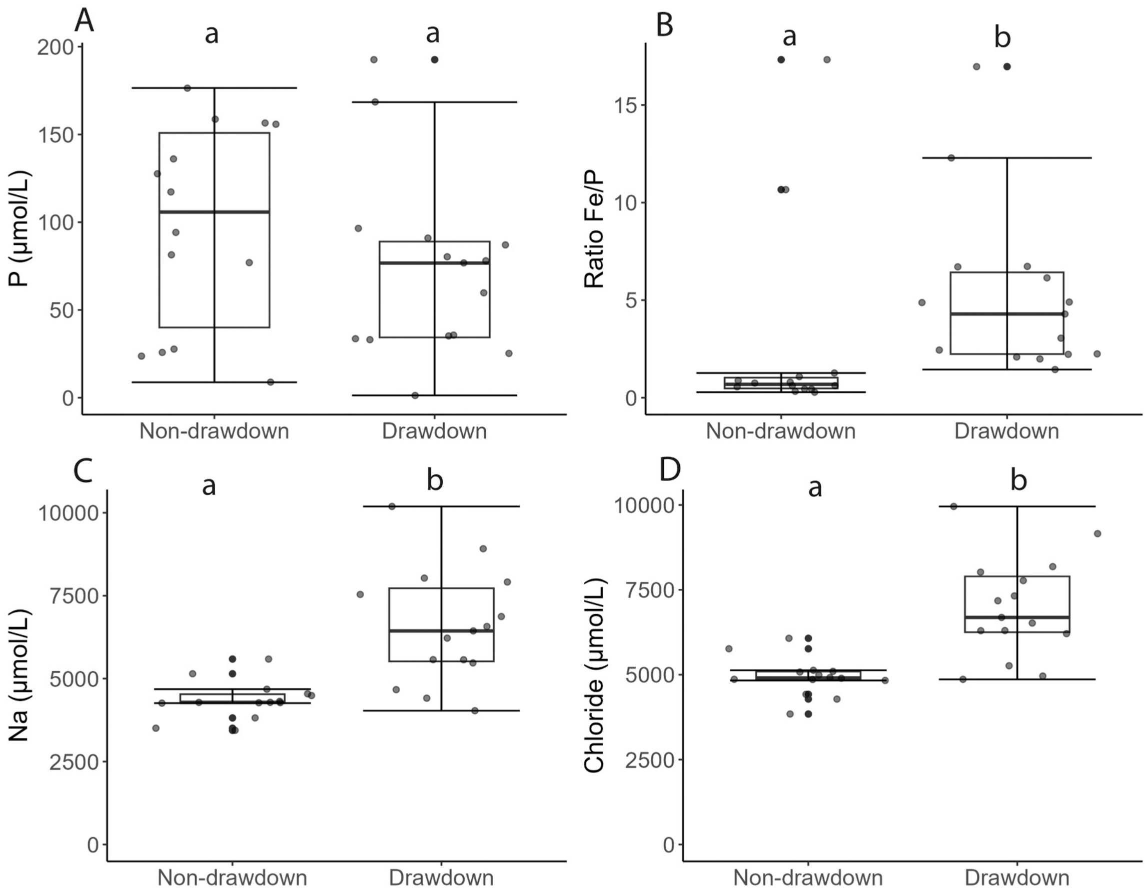


Fig. 3. Differences in nutrient concentrations in the porewater (A–D) at the start of the experiment from soils collected in non-water level drawdown and water level drawdown area (1-12-2020; $n = 15$). Boxplots show the median (middle line), quartiles (boxes), 1.5 times the interquartile range (IQR) (whiskers), and the individual data values (dots). Dots outside the whiskers are extreme values. Different letters indicate a significant difference ($p \leq 0.05$) between non-water level drawdown and water level drawdown. For statistical output, see Tables S6 and S7.

higher in the area with water level drawdown history ($p < 0.01$). For sediment nutrient concentrations, no differences were found for NH_4^+, NO_3^- P and alkalinity between both areas (Table S7; Fig. S8).

3.2. Part 2: water level gradient

3.2.1. Part 2.1: seed bank properties

In total 11,974 individuals germinated from 36 different species in the four sampled transects. Species richness decreased over the transect in both the area with water level drawdown history as in the area without water level drawdown history (respectively $X^2 = 14.43$, $p = 0.03$; $X^2 = 89.41$, $p < 0.01$; Table 1). Seed densities were higher on the 6th location compared to the 7th location ($t = 4.75$, $p = 0.04$) in the area with water level drawdown history. The area without water level drawdown history showed no increase in seed densities along the water level gradient ($X^2 = 13.77$, $p = 0.3$; after Tukey adjusted comparisons there were no more differences; Table 1). Diversity was higher at the locations with high elevation compared to the locations with low elevation ($X^2 = 21.189$, $p < 0.01$; Table 1) in the area with water level drawdown history. In the area without water level drawdown history no effect of water level gradient on diversity could be found ($X^2 = 15.2$, $p = 0.01$, after Tukey adjusted comparisons there were no more differences; Table 1). Mean germination was lower at the lowest elevational location in the area with water level drawdown history ($X^2 = 19.82$, $p < 0.01$; Table 1) compared to the 6th location along the water level gradient. In the area without water level drawdown history there was a higher mean germination on the 3rd location compared to the 5th, 6th and 7th ($X^2 = 23.468$, $p < 0.01$; Table 1). The permanova analysis showed no significant effect of gradient on species composition ($p = 0.57$; Figs. 4 and S4), while there was an increase in pioneer species in the seed bank of the area with water level drawdown history compared to the area without water level drawdown history ($p < 0.001$; Fig. 4). Within the two areas no effect was found of depth or gradient on species composition (Fig. S9).

Only transect 1, located in the non-water level drawdown area, showed a significant decrease in germination along the water level gradient (here plotted as the distance to the reed border, Fig. 5). Specifically, further away from the reed border where the elevation becomes lower we observe a decrease in germinated individuals (Fig. 5). Number of seedlings differed per transect from almost 2800 in transect 1 to four in transect 3. In the area without water level drawdown history, all transects showed near zero germination after circa 200 m from the established reed vegetation, in the area with water level drawdown history this approached 400 m.

3.2.2. Part 2.2 nutrient availability

In the area with water level drawdown history, increases in soil elevation across the water level gradient decreased soil ammonium availability in the sediment (negative rho) and increased sediment calcium and sulfur concentrations (positive rho) (Table S5). In the porewater, potassium, sodium and Fe:P ratio were lower with increased soil elevation, while calcium, magnesium and sulfur were higher (Table S2). The area without water level drawdown history showed a decrease with increased soil elevation (more amplitude in current water level fluctuations) for sediment potassium, magnesium and sulfur (Table S5). Porewater nitrogen, phosphorus and potassium were not affected, but

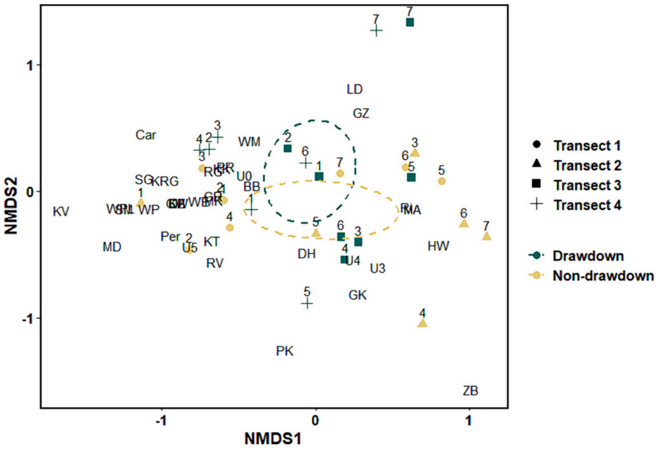


Fig. 4. Non-metric multidimensional scaling plot (stress = 0.13, dimensions = 3, Bray-Curtis dissimilarity) on the germinated plants for the four transects in both the area with water level drawdown history and the area without water level drawdown history ($n = 14$). Dotted lines represent the centroids of the groups and visualize the overlap in species composition. Different shapes represent the four transects and numbers depict the location within each transect (1 is relatively high elevation, close to the reed border; 7 is relatively low elevation, far away from the reed border). Transect 1 and 2 are located in the non-water level drawdown area (yellow color) and transect 3 and 4 are located in the water level drawdown area (green color). PERMANOVA analysis showed no effect of gradient ($p = 0.57$) but a significant effect of water level drawdown history ($p < 0.01$). The acronyms in the figure indicate different plant species. An overview of the plant species described by each acronym can be found in the additional information (Table S10).

calcium, iron, magnesium, silicon, Fe:P ratio and Fe:S ratio were higher at higher soil elevation (Table S2).

3.3. *Part 3: water level fluctuations*

3.3.1. *Part 3.1 seed bank properties*

During the water level manipulation experiment germination was low. In soil cores from the water level drawdown area only one *Typha (*spp.*)* germinated in the saturated treatment, while two *Ranunculus sceleratus* and one *Juncus effusus* germinated in the dry treatment. There was one unidentified plant that germinated in the saturated treatment. For the non-water level drawdown area only one *Zannichellia* spp. germinated in the wet treatment (Table S12).

3.3.2. *Part 3.2 nutrient availability*

After an experimental period of eight weeks, chloride and sodium porewater concentrations were increased by water level and water level drawdown history (concentration effect), while no effects were observed for porewater phosphorus and potassium (Fig. 6; Table S8; Figs. S6, S10). Highest Fe:P ratios were found in the saturated treatment from the non-water level drawdown area ($p < 0.01$), while the ratio was not affected by water level in the water level drawdown area. Specifically, concentrations of chloride and sodium were on average 2000 μmol/L higher in the area with a water level drawdown history (range averages 6000–10,400 μmol/L) than in the area without a water level drawdown history (range averages 4000–8200 μmol/L) after the water level manipulations. Chloride and sodium had the highest concentrations in the saturated > dry > wet treatments (Table S8). No differences were found in NH_4^+, NO_3^-, P, pH, alkalinity and acidification potential in the sediment between water level drawdown history and water level treatments (Table S7, Fig. S8).

4. Discussion

The objective of this study was to identify possible legacy effects of a water level drawdown on seed bank properties and nutrient availability in a human-managed eutrophic wetland. Our surveys and mesocosm experiment revealed that a previously induced water level drawdown, when interacting with the current water level fluctuations, indeed has a noticeable legacy effect on the seed bank. By contrast, the impact on nutrient concentrations is less pronounced. This indicates that inducing a water level drawdown in a eutrophic, clay wetland is successful to restart vegetation succession and replenishes the seed bank for a next water level drawdown without depleting nutrient availability.

4.1. *Water level drawdown history results in a more abundant seedbank with different species*

Our results show a higher number of germinated seeds in the area with water level drawdown history (30 years since last water level drawdown), which aligns with our hypothesis. Additionally, we found a decrease in seed abundances with increasing distance to the reed border which corresponds to lower elevational regions. This echoes other studies that show that water regime is the main determinant of seed bank properties (Casanova and Brock, 2000; Schneider et al., 2020). Specifically, a multi-annual water level drawdown or a partial dry period during summer, facilitates germination of seeds from the seed bank on the now exposed mudflats (Chow-Fraser, 1999; Coops and Hosper, 2002; Leck, 2003; Sarneel et al., 2014; ter Heerdt et al., 1996), which results in the establishment of pioneer species and subsequently perennial species. Perennial species are important to replenish the seed bank for a subsequent water level drawdown (van der Valk, 2013; Wienhold and van der Valk, 1989). While various studies support our findings (Capon and Brock, 2006; Wienhold and van der Valk, 1989), James et al. (2007) found an optimal frequency for flooding-drying cycles that maximizes viable seed densities. They argue that this is explained by a loss of seeds due to more frequent germination events in areas with high frequency in mudflat exposure due to water level fluctuations and an increase in non-viable seeds and scouring of the sediment in areas with a low frequency in mudflat exposure. These effects of current water level fluctuations on the soil seed bank can be highly variable and dependent on environmental conditions such as soil moisture (Haukos and Smith, 1994; Ter Heerdt et al., 2017; Van Leeuwen et al., 2014) and presence of seed-dispersing birds that are dependent on specific water depths (Farley et al., 2022; Kleyheeg et al., 2015). In our study, the transect along the elevational gradient, (e.g., changes in water level due to seasonal fluctuations) is directly related to the distance to the vegetation border. This means that, seed disposal events from the standing vegetation could interfere with the effects of water level drawdown frequency, caused by seasonal fluctuations in the water table. Overall, our results show a higher seed abundance in areas with water level drawdown history and at locations that are located relatively high within the water level gradient.

Our survey revealed that seed diversity was higher in the area without a water level drawdown history. In addition, we saw that water level drawdown history interacts with the water level gradient. In the area with water level drawdown history, locations at a relatively high elevation have a higher species diversity compared to locations at lower elevations. This trend was not observed for the area without a water level drawdown, where diversity was similar along the water level gradient. This indicates an interaction between water level drawdown legacy and the water level gradient. These results are partly in line with our hypothesis that predicted a higher seed diversity in the seed bank for both water level drawdown history and for locations higher on the water level gradient (more regularly exposed). Research findings on this subject diverge, ranging from an increased species count following water level drawdown (Casanova and Brock, 2000), to instances where no disparity in species count exists between areas with and without water level drawdown history (van der Valk, 2013), and, alternatively, reports of a decrease (Schneider et al., 2020). This can be explained by specific environmental conditions, such as moisture content (ter Heerdt, 2016;

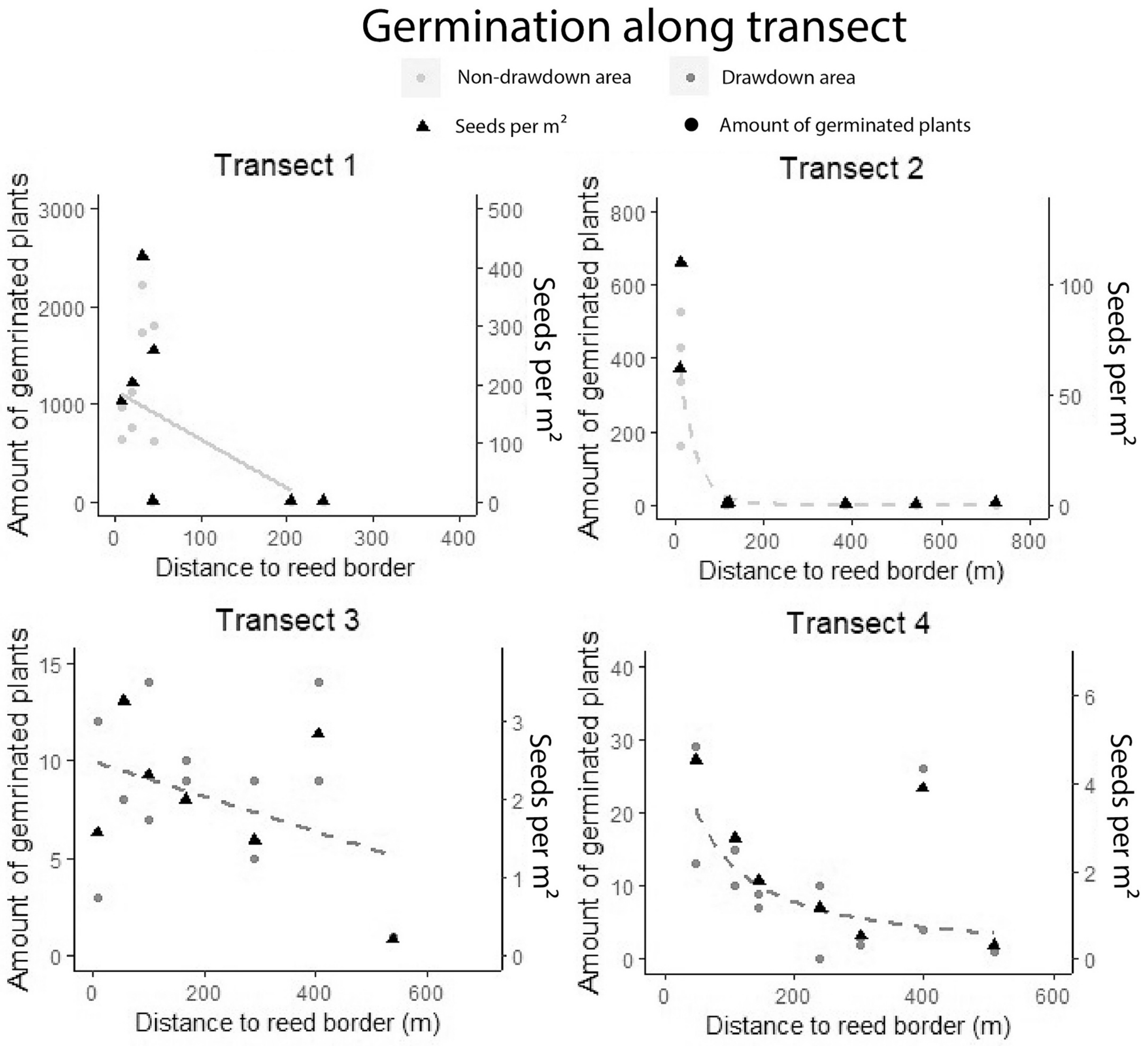


Fig. 5. Number of germinated plants (circles, $n = 14$) and number of seeds per m^2 (triangles, $n = 7$) along the distance to the reed border in meters. Best fit models (compared by AIC) were used to describe the relation between germinated plants and the distance to the reed border. (A) Linear decrease function for transect 1 ($p = 0.02$, $R^2 = 0.30$, RSE = 645.30), (B) exponential decay function for transect 2 ($p = 0.17$, RSE = 83.29), (C) Linear decrease function for transect 3 ($p = 0.10$, $R^2 = 0.14$, RSE = 4.50) and (D) hyperbolic function for transect 4 (a: $p = 0.10$, b: $p = 0.50$, RSE = 8.02). All exponential functions had an asymptote at 0. Note the differences in x and y-axis limits between the four plots.

Ter Heerdt et al., 2017; van der Valk, 2013; Van Geest et al., 2005; Van Leeuwen et al., 2014; Wilcox and Nichols, 2008). These environmental conditions select certain species to germinate, thereby lowering species diversity in the seed bank to only the species tolerant to these conditions, and the species that can complete their life cycle (Van Geest et al., 2005; van der Valk, 2013; Wilcox and Nichols, 2008). This mechanism was found for frequently flooded habitats in other wetland systems (Capon, 2005; James et al., 2007), but could also hold true for droughts. The lack of an impact of the water level gradient on seed diversity in the area without water level drawdown history may be attributed to the substantial presence of germinated water speedwell (*Veronica anagallis-aquatica*), reaching up to 2000 individuals per location. Such high numbers greatly affects diversity in these samples. Overall, our results show no legacy effect of water level drawdown history on seed diversity, while water level gradient alters this parameter albeit with high location-specific variety.

Our data show that species composition differs with water level drawdown history, but not along the water level gradient. This is partly in line with our hypothesis, where we expected varying species compositions for both water level drawdown history and along the water level gradient. The primary mechanism at play appears to be that seed bank replenishment occurs exclusively through species that complete their life cycle. Consequently, these species can also influence the overall species composition following a water level drawdown event (Capon, 2005; James et al., 2007). This indicates that even a single long-term water level drawdown event with strong environmental filters could skew the seed bank composition to the dominant plant species present during a consecutive water level drawdown. Indeed, the standing vegetation diversity highly correlates with the diversity of the seed bank (Ter Heerdt et al., 2017). The lacking response of species composition to current water level fluctuations in our survey could relate to wind and wave action combined with very soft sediment, which distributed seeds throughout the area creating a relatively homogeneous seed bank (Haukos and Smith, 1994; Van Leeuwen et al., 2014). On the other hand, the timing of a water level drawdown can also influence the species that are able to germinate and set seed, which in turn contribute to the future seed bank pool (Ter Heerdt et al., 2017). Grace (1987) showed that small differences in the timing of a water level drawdown,

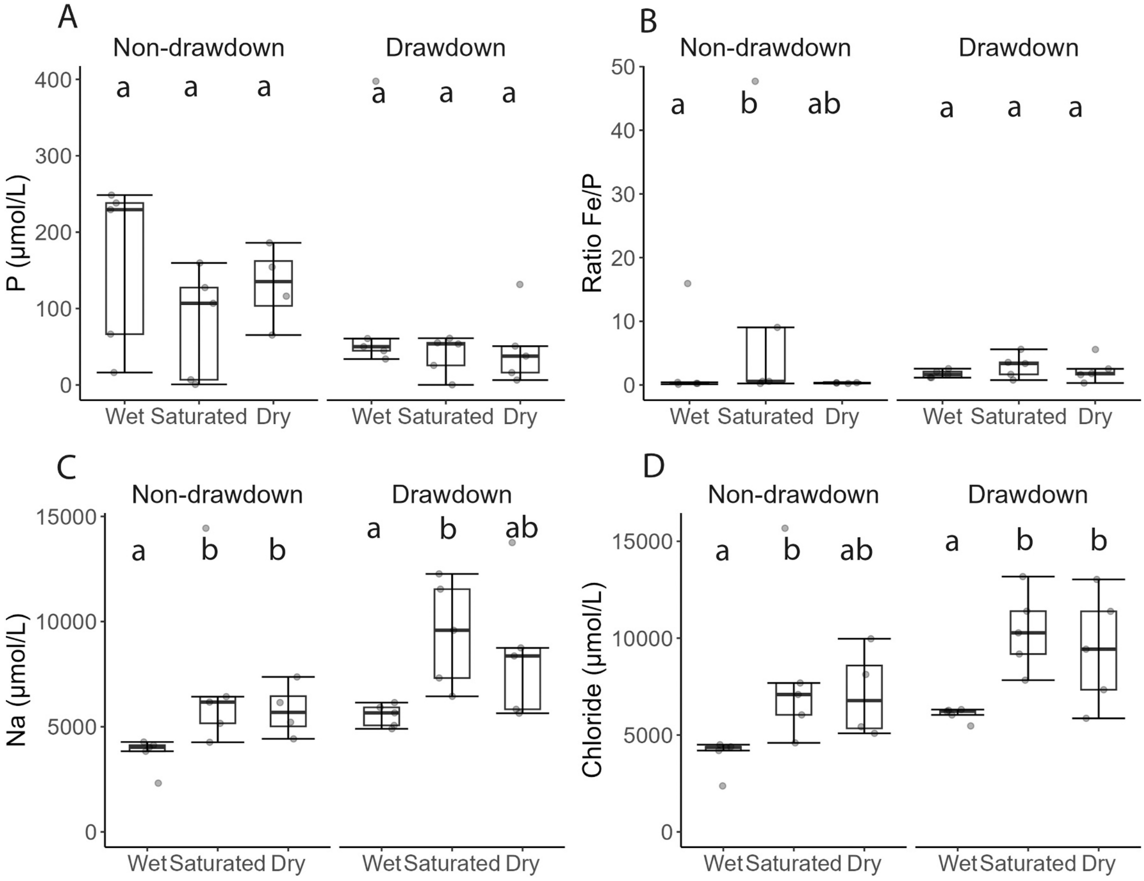


Fig. 6. Boxplots of the nutrient concentrations in the porewater (A–E) and the sediment (F) collected at non-water level drawdown and water level drawdown areas for the three treatments (Wet, Saturated and Dry) at the end of the experiment (26-1-2021; $n = 5$). Boxplots show the median (middle line), quartiles (boxes), 1.5 times the interquartile range (IQR) (whiskers), and the individual data values (dots). Dots outside the whiskers are extreme values. Different letters indicate a significant difference ($p \leq 0.05$) between water levels separately for non-water level drawdown and water level drawdown areas. For statistical output, see Tables S7 and S8.

e.g., one week, could already alter future responses. However, in our study this does not seem to be the case, because species composition remained similar along the water level gradient, even though the seasonal variation in precipitation and evaporation in combination with the elevational differences along this gradient could have led to changes in timing of water level drawdown. A possible explanation might be that the variance in sediment elevation within one transect is too small to affect the timing of water level drawdown or that the environmental conditions (e.g., weather conditions) at the moment of mudflat exposure were very similar to each other, leading to selection of the same species along the transect. In general, we see a legacy effect of a multi-year water level drawdown event on the species composition but no effect of the water level gradient on species composition in the seed bank in general.

To further investigate the effect of water level drawdown on species composition in the seed bank, existing literature on the seed bank in our study area after the water level drawdown event was compared to the present-day results. Interestingly, most species found in our study were also present in the previous studies (ter Heerdt et al., 1996; Ter Heerdt and Drost, 1994; Vonk et al., 2017). However, in the different studies (e.g., over time) changes occurred in relative abundances of each species (ter Heerdt et al., 1996; Ter Heerdt and Drost, 1994; Vonk et al., 2017) (Table S13). This change in species composition and dominant species between studies might be caused by the longevity of the seeds. Some seeds were rather short-lived and might therefore be depleted from the species pool over this 30 year period. Another important mechanism is the ability for species to set seed during the years of higher water level, which might lead do a relatively higher contribution of seeds from e.g., more water tolerant species over time.

For the water level manipulation experiment, germination was too low to statistically analyse the results, even though the trend seems to support the earlier results, since 5 out of 6 germinated plants originated from the water level drawdown area. The lack of high germination rates compared to the germination experiment could be caused by the use of intact soil cores instead of aiming for optimal germination conditions, including disturbing the soil to allow seeds from deeper sediment layers to germinate (ter Heerdt, 2016). Additionally, it could be that the applied water level treatment inhibited the germination of some of the seeds, also limiting the total number of seedlings observed (Vonk et al., 2017).

4.2. Water level drawdown history and water level gradient affect nutrient availability

Our mesocosm experiment demonstrated that nutrients were affected by water level drawdown history, but were generally high compared to other aquatic systems (Markermeer in Jin et al., 2023; Great Lakes in Mahdiyan et al., 2021; and see Geurts et al., 2008). These results are only partly supporting our hypothesis, in which we expected a decrease in nitrogen and phosphorus concentrations due to increased oxygenation of the sediment. Phosphorus availability is probably lower due to improved binding in the soil as a result of oxygen intrusion into the sediment during the water level drawdown (Lamers et al., 1997, 1998; Vonk et al., 2017). However, concentrations remain high and therefore these differences are most likely ecologically not relevant. The experiment did, however, not show an impact of the eight-weeks water level drawdown on nutrient availability, unlike other literature with similar time frames (Vonk et al., 2017). We assume that the limited availability of Fe in these sulfur-rich (formerly marine) areas, combined with high phosphorus concentrations and large variation, was insufficient to bind phosphorus in this time span. Furthermore, the saturated treatment had higher Fe:P ratios and a very high sulfur concentration, potentially leading to more sulphide binding to iron, which would lead to higher P availability in the pore-water. Therefore, it is also expected that there is not a large phosphorus flux from the pore-water to the surface water after rewetting (Fe:P ratio is 15, while below 1 is an indication of large flux) (Loeb et al., 2008).

Water level drawdown history affected sediment ammonium concentrations by reducing it to half the concentrations found in the area without water level drawdown history, and concentrations were also lower at locations with a higher mudflat exposure (e.g., higher soil elevation, closer to the reed vegetation) for the water level drawdown area. This is in agreement with our hypothesis. A possible explanation is that the penetration of oxygen during the water level drawdown led to the coupling of nitrification and denitrification, resulting in nitrogen removal from the system in the form of nitrogen gas (both N_2 and NH_3) (Sollie, 2007). Short-term water table water level drawdown in the experiment did, however, not lower nitrogen availability. Even though this decrease is observed, ammonium concentrations remain high and therefore no limitation for plant growth is expected.

Although differences in phosphor and nitrogen concentrations were observed between the two areas, they, however, did not drastically decrease as hypothesized. We realize that the outcome might change when focusing on the analysis of different forms of phosphorus (Loeb et al., 2008; Lucassen et al., 2005; Wang et al., 2020) or the potential different transformation pathways of nitrogen (Cavanaugh et al., 2006; Howard-Williams, 1985; James et al., 2004; Lamers et al., 2012), however our measurements do not allow such further analyses. The high sulfur contents in the pore-water may create a high chance of acidification of the system upon water level drawdown. However, buffering capacity, indicated by the $\frac{S}{Ca+Mg}$ ratio, of the system as a result of the high calcium contents remained well below 0.667, which is described as the threshold value below which the buffering capacity of the system should be sufficient (Lucassen et al., 2002). Overall, these results indicate that the legacy effects of a water level drawdown on nutrient availability, also with regard to potassium, seem limited. This implies that in a eutrophic wetland there is no direct negative effect of a water level drawdown on nutrient availability and subsequently productivity.

4.3. Conclusions & implications

A water level drawdown in a wetland drives natural processes, including the germination of pioneer vegetation on exposed sediment and biogeochemical cycling. These processes are essential for wetland functions, particularly in supporting bird populations. In human-managed wetlands with no natural, multi-year water level dynamics, artificially inducing water level drawdowns might be vital to create a long-term biodiverse wetland system. These human-induced water level drawdowns are being applied in various wetlands worldwide, including the human-made wetland Oostvaardersplassen in the Netherlands, (Vulink and Van Eerden, 1998), the brackish wetland Dowd Moras in South-Eastern Australia (Raulings et al., 2011) and the Montezuma wetland complex near New York, USA (Farley et al., 2022). Our field survey and experiment highlight that the legacy effects of a water level drawdown are mainly reflected in the number of viable seeds present in the seed bank and with regard to the species composition of the seed bank. The legacy effects on nutrient availability, although present, remained less pronounced due to in general high nutrient availability in the area. This indicates that such a water level drawdown could be used as a restoration measure without jeopardizing ecosystem functioning in a eutrophic wetland system. We suggest that attention should be paid to the water level drawdown frequency and the long-term effects on the seed bank, as species might be lost that have a limited seedbank longevity.

In natural wetlands characterized by seasonal and long-term water level dynamics, human-induced water level drawdowns are not necessary, and in degraded ones, we argue that restoration of natural dynamics has priority over artificial water level drawdowns. However, when this is not possible, inducing water level drawdowns might be a viable tool to recreate near-natural dynamics that facilitate long-term functionality of wetlands. Global changes in climate and land use call for a better understanding of the effects of frequency of a water level drawdown and its long-term effect on the seedbank, vegetation, and nutrient dynamics and warrants future research to better anticipate changes on natural and human-managed wetland systems.

CRediT authorship contribution statement

Kerstin Bouma: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Elisabeth S. Bakker:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition. **Marleen Wilborts:** Writing – review & editing, Methodology, Investigation. **Bjorn J.M. Robroek:** Writing – review & editing. **Leon L. Lamers:** Writing – review & editing. **Perry Cornelissen:** Writing – review & editing. **Mennobart R. van Eerden:** Writing – review & editing. **Ralph J.M. Temmink:** Writing – review & editing, Writing – original draft, Methodology, Investigation.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Kerstin Bouma reports financial support was provided by Vereniging van Bos- en Natuurterreineigenaren. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is available on DataDryad (http://datadryad.org/): DOI: 10.5061/dryad.z08kprrnc.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.172531.

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