Status of plant-available potassium after 17 years of wet grassland restoration on a degraded minerotrophic peat soil

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SUMMARY

Potassium availability is an important regulator of plant species composition and ecosystem productivity. Hence, potassium plays a crucial role when the aim is to produce notable quantities of roughage in wet grassland farming. The objective of this case study was to elucidate the long-term dynamics of plant-available potassium (K_{DL}) in a seasonally rewetted peatland in the Dümmer lowland in northwest Germany. This study investigated the effects of three grassland management systems and the impact of greatly fluctuating water levels on the K_{DL} content. Over a period of 17 years, four sampling campaigns were conducted across the study area. The most remarkable result was that strong discontinuous nutrient dynamics were observed over time. In the early years, the varying nutrient pathways of the three grassland systems significantly determined K_{DL} content. Over time, the grassland effects decreased, while the effect of seasonal rewetting on K dynamics increased. After 17 years, all the grassland systems showed a similar very high K_{DL} content. This was probably due to a periodical recharge of the K_{DL} stocks by seasonal inundation events. Therefore, successful nutrient management should consider specific land-use effects as well as the heterogeneous dynamics and water quality of seasonal flooding events.

KEY WORDS: extensive management, fen, Histosols, nutrients, rewetting

INTRODUCTION

Ecosystem productivity is generally constrained by nutrient limitation (Fay *et al.* 2015, Smithwick *et al.* 2016). Consequently, nutrient availability influences plant growth and species composition (van Duren & Pegtel 2000). In wet grassland ecosystems, the dynamics of available nutrients are further affected by water regulation (Koerselman *et al.* 1990b, van Duren & Pegtel 2000). In contrast to other macronutrients, the dynamics of potassium (K) has to date received relatively limited attention due to the fact that a surplus of K does not contribute to the eutrophication of aquatic ecosystems (Johnston & Goulding 1988, Kadlec & Wallace 2009).

However, K is an essential element of plant growth and plays a vital role in physiological and essential metabolic processes (Marschner 2012). Furthermore, a sufficient supply of K will contribute to more efficient plant uptake of other macronutrients (Johnston & Goulding 1988, Koppisch *et al.* 2001) and is thus crucial to successful restoration management on degraded peatland.

In agricultural systems, the range of soil K is primarily controlled by parent material, soil type, mineralogy and land-use history (Sparks 1987, Johnston & Goulding 1988). The typical content of total K in mineral arable soils varies from 0.04 to 3.3 % of total soil mass (Sparks 1987), where a substantial proportion of the total K pool is fixed in several primary minerals (e.g. alkali feldspars and micaceous minerals) and becomes available for plant growth very slowly (Sparks 1987, Öborn *et al.* 2005). In contrast, most peat soils (Histosols) have poor K contents of 0.02 to 0.35 % of total soil mass (Verhoeven 1986, Vitt & Chee 1990). This can be explained by the low K-holding capacity of the accumulated peat-forming substrate (Verhoeven 1986, Hietz 1992, Bragazza *et al.* 2007) and the absence of K-bearing minerals in most mire types

(Mengel & Kirkby 2001). However, organic peat tissue in Histosols has an intrinsic high cation exchange capacity (CEC) that is comparable to mineral phyllosilicates (Hobbs 1986, Lax *et al*. 1986, Verhoeven 1986). Secondary peat decomposition in particular may increase the number of carboxyl and phenolic groups and promote the absorption of cations (Puustjarvi & Robertson 1975, Lax *et al.* 1986, Kyziol 2002). However, K is still highly susceptible to leaching losses. The presence of divalent and multivalent cations in the soil solution displaces monovalent K cations at binding sites and drives massive translocation of K under free drainage conditions (Mundel 1992, Kadlec & Wallace 2009). Additional amounts of K are taken up by plants and the annual K offtake by hay mowing varies greatly from 30 to 150 kg ha $^{-1}$ (Benke & Isselstein 2001, Olde Venterink *et al.* 2002b). Hence, a short supply of plant-available K can present an obstacle when the aim is to produce profitable quantities of fodder grasses under both drained and waterlogged conditions.

Previous work on K in Histosols has often focused on short-term nutrient dynamics and the impact of K depletion on species diversity and plant biomass production (Kapfer 1988, Eschner & Liste 1995, Pöplau & Roth 1995, Oomes *et al.* 1996, Oelmann *et al.* 2009). Moreover, laboratory incubation experiments have shown no clear effects of water saturation level on K remobilisation. Olde Venterink *et al.* (2002a) found a strong decrease in plant-available K in both permanent wet and slowly desiccated peaty soil samples. In incubation studies by Koerselman *et al.* (1993), plant-available K in pure *Carex* peat was significantly affected by water chemistry and differences in water levels, but the trends in K solubility were inconsistent.

The stock of available K in Histosols appears to be affected by a number of factors, including seasonally oscillating water tables and the occurrence of flooding events, alterations in water chemistry, and changes in grassland management. This situation calls for surveys over longer periods of time that also consider the effects of different management practices on K dynamics. Therefore, the aims of this 17-year study were: (1) to investigate the long-term dynamics of plant-available potassium content (K_{DL}) on a seasonal rewetted fen peatland; (2) to analyse the effects of different grassland management systems and rewetting time on K_{DL}; and (3) to elucidate the role of peat degradation on the content of K_{DL}. This article contributes to improved understanding of the complex nutrient pathways during rewetting measures and thereby supports management decisions concerning semi-natural, wet grassland habitats.

METHODS

Study area

The study area Osterfeiner Moor (52° 33' 19.17" N, 8° 20' 25.68" E) is located in the Dümmer lowland in northwest Germany (Figure 1). It comprises 173.7 ha of protected wet grassland and is partitioned into 50 fields varying in size from 0.43 to 7.23 ha (average 2.86 ha). The maritime climate is characterised by average annual precipitation of 713 mm and an average annual air temperature of 9.6 °C (1981–2010; station Diepholz 963 (DWD 2020b)). Since the Boreal age, the sprawling wetland on the margins of Lake Dümmer have resulted in the formation of predominantly sedge peat (Pfaffenberg & Dienemann 1964). From the 12th century, the open water transition fen was gradually cultivated into pasture and drained arable land. Lake Dümmer has been regulated by a dyke since 1953 to reduce flooding. In the subsequent three decades, agricultural use and nutrient input increased steadily. In 1999, the study area was converted into a meadow bird conservation area and adapted rewetting measures and wet grassland management were implemented. In the summer, free drainage conditions are adjusted to facilitate the area's agricultural management and trafficability.

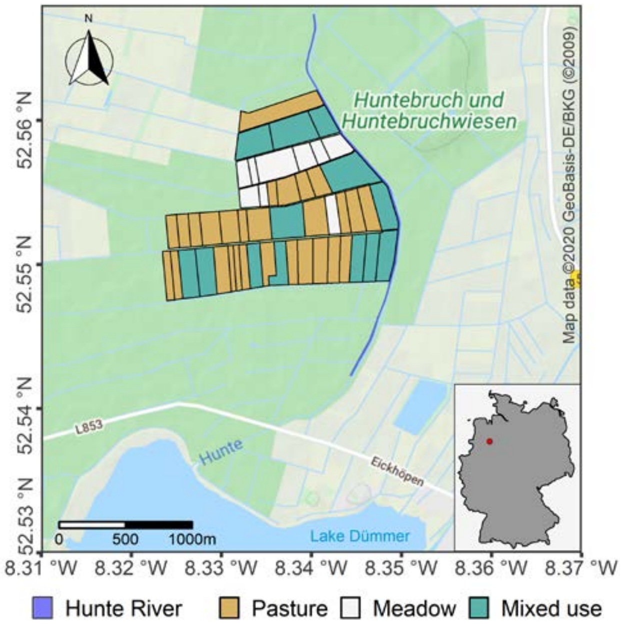

Figure 1. Map of the Osterfeiner Moor study area in northwest Germany (red point), highlighting different grassland management practices and the Hunte river (Google Maps; Kahle & Wickham 2013).

Grassland management

The grassland fields have been extensively managed in three ways: as meadow (cutting only), as pasture (grazing only) and as a mixed system (combination of cutting and subsequent grazing). Other management restrictions include no input of nutrients by organic or mineral fertiliser, no additional fodder application, a low stocking rate limited to <1.2 livestock units per ha, and a first cutting only from July onward. Grassland management has been randomly distributed across the area due to the lease or tenure history of the field units (Figure 1).

Management and modelling of the water table

Drainage in the Osterfeiner Moor is controlled by three main ditches running west to east that empty into the adjacent Hunte river. Since 2000, peat-preserving water management has been practised in the study area. This includes the seasonal blocking of all ditches from November to April. Water table levels are measured hourly in nine observation wells in the study area. An additional well has been inserted in a ditch in the west of the study area. All the observation wells are equipped with a diver data logger (company: Van Essen).

Water table data were recorded from December 1999 to January 2006 and from November 2016 to November 2018. In 2006 and 2016, manually measured water levels in the ditch system were used to model water table levels throughout the study area. These data formed the basis for modelling the monthly water table levels in the study area (using the central fields) using the SWAP ecohydrological model (Kroes *et al.* 2017) and the FREEWAT groundwater flow model (Rossetto *et al.* 2015). First, the water table point data were modelled with SWAP with the input of meteorological data (German Weather Service; station Diepholz 963) and soil physical data for the area, plus additional data on drainage characteristics. The model was verified by the single point diver data of the observation wells. Second, the water table level was calculated over the area for the period 2001–2018 with the groundwater flow model FREEWAT using soil physical parameters, groundwater recharge rate and water levels in the ditches.

To determine WTD (water table depth: difference between ground level and water table level), the ground level of each field was manually estimated in 2001 on 1,108 terrain points. In 2017, the ground level was measured again by a georeferenced orthophotograph (Hofer & Pautz GbR). The orthophotographs were recorded in January 2017 with 88 individual values per square metre. It was assumed that the soil was highly water saturated during this time and that the organic soil horizons had expanded to their maximum. These data were used to generate a digital terrain model with grid cells of 5 m.

Soil sampling, analysis and classification

The soil sampling campaigns were conducted in the month of November in 1999, 2003, 2005 and 2016. In each sampling year, a representative topsoil sample (0–10 cm) from each field was obtained by mixing at least seven sub-samples per ha. Immediately after sampling, the soil samples were cooled and stored at 4–6 °C until further chemical analysis. The plant-available K content of all soil samples was analysed using the double-lactate method (VDLUFA 1991b, Otabbong *et al.* 2004). In Germany, this method is used to assess the soil fertility status of various macronutrients (e.g. K_{DL}, P_{DL} & Mg_{DL}) in agricultural soils and thus, in accordance with this method, the air-dried and sieved samples (≤ 2 mm) were extracted with a calcium-lactate solution ($C_6H_{10}CaO_6 \cdot 5\ H_2O$, approximately 0.3892 moles L^{-1}; adjusted with hydrochloric acid at pH 3.6) using a solution-soil ratio of 20:1. The K content of the soil extracts (duplicates) was then determined with a flame photometer (Flame Photometer 410, Sherwood Scientific Ltd) at a wavelength of 767 nm. Lactate extraction is a measure used to determine the soluble K present in soil pore water and the readily exchangeable K pool bound to the soil particle surface that directly contributes to plant nutrition (Binner *et al.* 2017). In the absence of clay minerals, the difference in the soil K extraction power of routinely applied extractants (NH_4 acetate, Ca-lactate, $CaCl_2$, etc.) is only marginal (Mc Lean & Watson 1985, Binner *et al.* 2017). Similarly, the use of dried or moist peat soil samples has no effect on the K_{DL} extraction behaviour (Kuntze 1980). The pH values were measured for each soil sample. Moist soil samples were sieved (4 mm) and a sample volume of 20 ml was suspended in 50 ml of 0.01 M $CaCl_2$ solution. The soil water suspensions were allowed to stand for one hour with occasionally stirring before measurement (VDLUFA 1991a). The ash content of each sample was determined (singular) using the loss-on-ignition method (LOI_{550}) by combusting 10 g of milled soil at 550 °C for 4 h (Wright *et al.* 2008). The ash content estimated the mineral soil constituents and may provide additional information about the degradation status of the already advanced decomposed peat (sapric) in the study area. The total carbon (C) and nitrogen (N) content of the different soil horizons was determined by duplicate measurements with a pyrolysis CNSOH analyser (Elementar vario PYRO cube) at a furnace temperature of 1500 °C. The corresponding C/N value was calculated from the mass relationship between the carbon and nitrogen content of the samples.

As well as topsoil sampling, ten representative soil profiles (0–100 cm) were classified in 2016 according to the World Reference Base (IUSS Working Group WRB 2015) and the German soil classification KA5 (Ad-Hoc-AG Boden 2005). Fresh peat samples were used to visually estimate the state of degradation using the von Post scale (Jordan *et al*. 2007). In a ten-class scale (H1–H10), the von Post field method describes the degree of decomposition of the organic peat constituents (Klavins *et al*. 2008).

Statistical analysis

A two-way ANOVA was used to test for the effects of the long-term dynamics of rewetting time (0, 4, 6 and 17 years), grassland management (meadow, pasture and mixed use) and the interaction of these two factors on the K_{DL} content of the topsoil. A Tukey-HSD post-hoc test with a Sidak confidence level adjustment was applied to produce multiple comparisons of K_{DL} means. A Kruskal-Wallis test was also performed on K_{DL} content, as influenced by the type of grassland management for the last survey year (2016). The relationship between the peat ash contents and K_{DL} was assessed by Pearson's correlation analysis. Subsequently, an ordinary least squares regression was conducted, presented as a scatterplot with a trendline following a fitted linear regression model with a 95 % confidence interval. The statistical software package R was used (R Core Team 2019) for all statistical analyses.

RESULTS

Peat soil classification

After continuous drainage and intensive agricultural use in the last century, the peat in the study area showed strong characteristics of decomposition. The peat structure in the topsoil of the ten soil profiles was found to range from amorphous fine-grained to dust-like, with no recognisable plant structure. Accordingly, the von Post decomposition level was determined as H10 in the topsoil of all the soil profiles. Deeper soil horizons showed slightly less degradation and the level of humification ranged from H8 to H10 (Table 1). Peat horizons in the soil profiles had a thickness of 0.27 to 0.48 m and were shallow and consolidated. Below the sapric peat horizon (KA5: amorpher Torf), algal gyttja (KA5: Lebermudde) was found, and in deeper sediments calcareous gyttja (KA5: Kalkmudde) occasionally occurred. According to the WRB classification system, this peat soil can be classified as a Rheic Murshic Histosol (Limnic), which corresponds to a 'Mulmniedermoor' in the German KA5 soil classification. Detailed information on the soil profile characteristics can be found in Table 1.

Trend of water table depth

The trend of water table depth was influenced by the quantity and distribution of precipitation in both the summer (May to October) and winter seasons (November to April). In particular, inter-seasonal precipitation rates of over 760 mm (winter + summer precipitation) could lead to higher WTD in winter

Table 1. Summary of the main peat characteristics from ten soil profiles. The soil was sampled in November 2016 and classified according to KA5 (Ad-Hoc-AG Boden 2005). Numerical data are given as mean ± standard deviation.

Horizon KA5	Horizon (cm)	Sediment type (KA5 class)	von Post	Munsell colour	LOI_{550} (%)	C_T (%)	N_T (%)	C/N
nHm to nHv	12 ± 3	amorphous peat (amorpher Torf, Ha)	H10	10YR 2/2	76.3 ± 6.2	44.4 ± 3.8	2.7 ± 0.2	17 ± 2
nHa	16 ± 8	amorphous peat (amorpher Torf, Ha)	H8–H10	10YR 2/2	75.9 ± 6.6	45.6 ± 4.6	2.5 ± 0.2	18 ± 2
nHt	14 ± 4	amorphous peat (amorpher Torf, Ha)	H8–H10	10YR 2/2	84.1 ± 2.2	48.7 ± 4.6	2.8 ± 0.2	18 ± 2
II fFr	24 ± 12	algal gyttja (Lebermudde, Fhl)	-	2.5Y 2.5/1	81.3 ± 3.0	45.1 ± 4.8	2.9 ± 0.4	15 ± 3
III feFr	23 ± 11	calcareous gyttja (Kalkmudde, Fmk)	-	2.5Y 6/1	32.4 ± 8.4	23.9 ± 1.7	1.4 ± 0.2	17 ± 2

(Table 2). Corresponding precipitation rates caused long-lasting flooding events in the winter seasons of 2001/02, 2002/03 and 2015/16 (Figure 2). These flooding events were characterised by water levels of up to 20 to 40 cm above the soil surface. In contrast, a lower WTD occurred in the winter seasons of 2003/04, 2004/05 and 2005/06, all with inter-seasonal precipitation rates of less than 640 mm (Table 2). Generally, WTD in the summer seasons was much lower due to high evapotranspiration rates and adjusted free drainage conditions.

The distribution of the highest WTD for the year 2017 is given in Figure 3a. The fields along the central south to north axis in particular showed WTD values above the soil surface. In the southeast fields, WTD values were below the soil surface and decreased towards the Hunte river as well as towards the southwest fields. The surface area in these parts of the study area is slightly elevated in comparison with the centre or north of the study area.

Table 2. Mean water table depth (WTD), precipitation rates and groundwater recharge rates (GRR) of the study fields (n = 50). The balance year is from 1 May to 30 April of the following year. The WTD is given as mean ± standard deviation. All climate data were provided by DWD Climate Data Centre (Diepholz - ID 963; DWD (2020a) and DWD (2020c). GRR is the sum of precipitation and negative potential evaporation (Haude 1954).

Balance year	WTD (m)	Precipitation (mm)	GRR (mm)
2001/02	0.25 ± 0.17	802	238
2002/03	0.27 ± 0.16	785	231
2003/04	0.47 ± 0.16	599	-67
2004/05	0.44 ± 0.16	632	79
2005/06	0.42 ± 0.18	639	70
2015/16	0.14 ± 0.20	769	205
2016/17	0.27 ± 0.25	537	-98

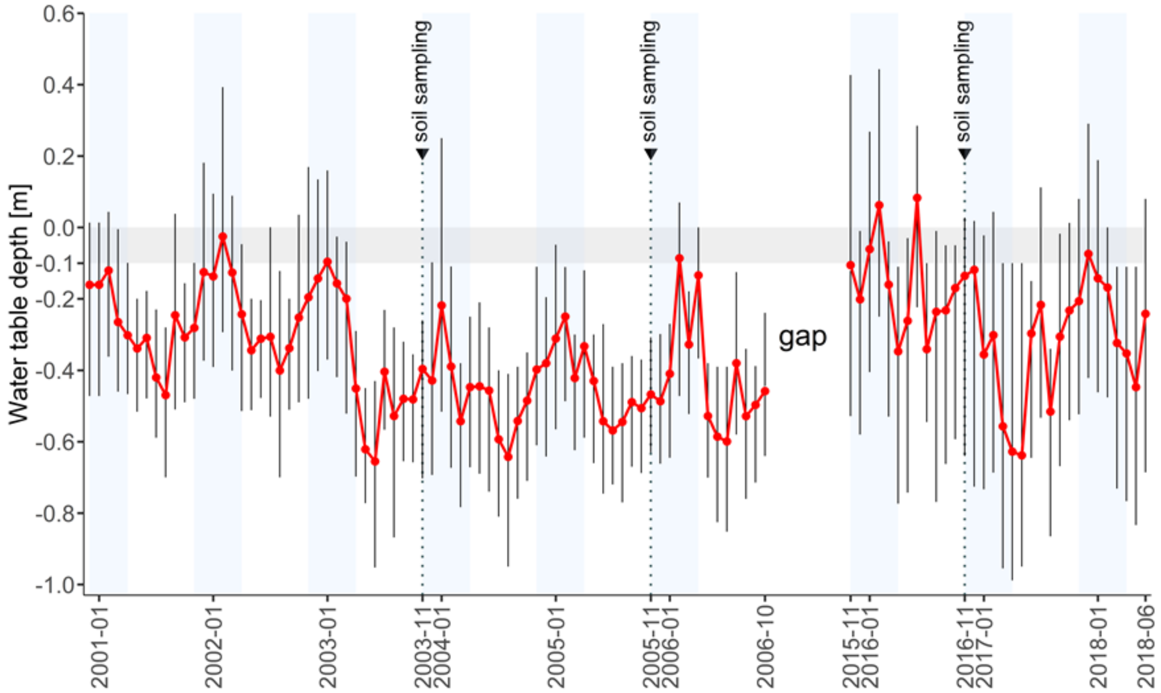

Figure 2. Trend of monthly mean WTD (red dots) and min-max WTD (black vertical bars) of the study fields. The light blue shaded sections show the winter season with blocked ditches (November to April).

Influence of rewetting time and type of grassland management on K_{DL} dynamic

A significant effect of rewetting time was found on the overall K_{DL} content (two-way ANOVA: $F = 28.6$, $p < 0.001$), but K_{DL} content showed a strong dynamic over the years (Table 3). Before the rewetting measures were implemented, the mean K_{DL} content in November 1999 was 29.8 mg 100 g^{-1} (Table 4). In 2003, the K_{DL} content reached a maximum of 34.3 mg 100 g^{-1} and fell to 17.9 mg 100 g^{-1} in 2005. In 2016, the mean K_{DL} content of 30.1 mg 100 g^{-1} was similar to the initial level. Surprisingly, although no fertiliser was applied, only the K_{DL} content in 2005 was significantly lower than in the other survey years. Between 2003 and 2005, the K_{DL} stock decreased by 69 kg ha^{-1}, while in the other periods (1999–2003 and 2005–2016) K_{DL} stocks increased by 11 and 38 kg ha^{-1} respectively. Figure 3b shows the distribution of K_{DL} content between the fields in 2016. The slightly increased K_{DL} content in the central fields should be noted, as well as the strongly elevated values in the southeast riparian fields.

The type of grassland management also had a significant effect on the K_{DL} content of the topsoil (two-way ANOVA: $F = 3.8$, $p = 0.024$). The meadow fields had significantly lower K_{DL} contents in the

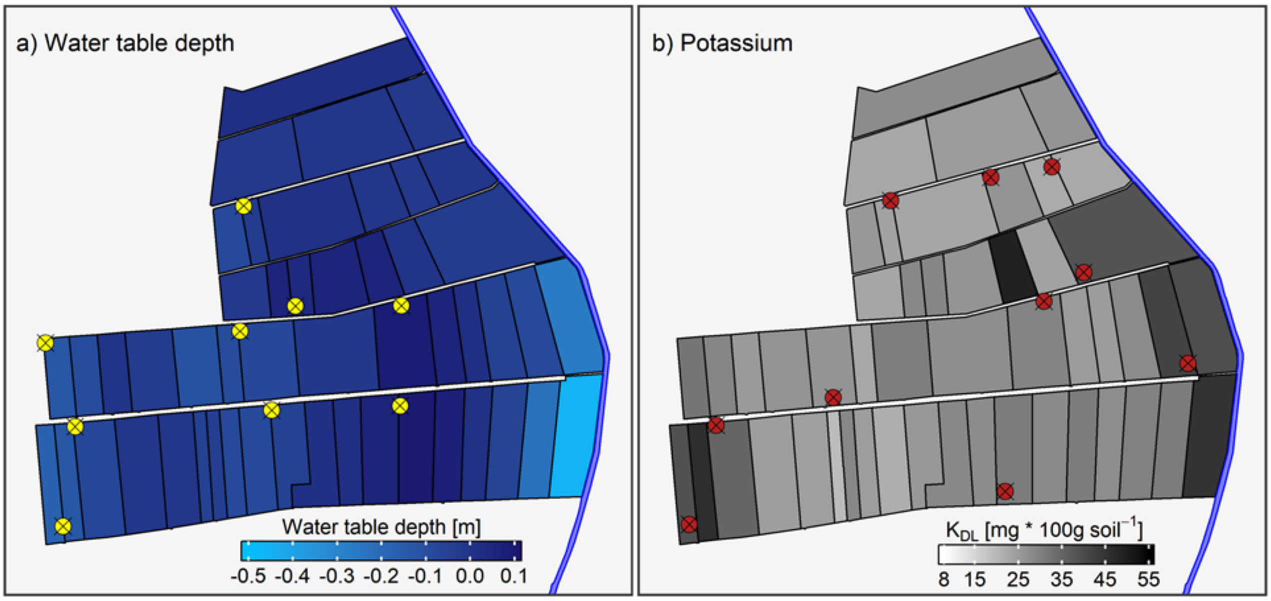

Figure 3. Left (a): the distribution of the highest water levels in 2017 and the nine observation wells (yellow points). Negative values of (increasingly light blue) indicate water levels below the soil surface. Right (b): the distribution of K_{DL} in 2016 and the position of the ten soil profiles (red points).

Table 3. K_{DL} content in the topsoil (0–10 cm) after different periods of rewetting (0–17 years) and for different types of grassland management (meadow, mixed use, pasture). The last column indicates significance levels (p) for the differences between K_{DL} means: '***' $p \leq 0.001$, '**' $p \leq 0.01$, '*' $p \leq 0.05$; n.s. = not significant ($p > 0.05$). df = degrees of freedom, F = F-test value.

Source of variation	*df*	Sum of squares	*F*	*p*
Rewetting time	3	20.450	28.56	< 0.001 ***
Grassland management	2	1.808	3.80	0.024 *
Time × Management	6	1.899	1.33	0.246 n.s.
Totals	188	44.734		

topsoil than the mixed use and pasture grassland (Table 4). The interaction 'Rewetting time x Type of grassland management' was not significant (two-way ANOVA: F = 1.33, p = 0.246). After 17 years of restoration measures, in the final survey year there was no difference in K_{DL} content between the types of grassland management (Kruskal-Wallis-test: X^2 [df = 2, n = 50] = 0.262, p > 0.05).

Development of K_{DL} dynamic under grassland management

Before the rewetting measurements were implemented, mean K_{DL} content of 31.1 mg 100 g^{-1} were found in the pasture fields (Figure 4). Within the first four years, the mean K_{DL} content increased by 26 % on pasture fields and decreased significantly by 56 % in subsequent years. After 17 years of grazing,

Table 4. Two-way ANOVA results of transformed K_{DL} values. The influence of rewetting time, type of grassland management and the interaction of both variables on K_{DL} contents (topsoil, 0–10 cm) was examined. Different letters (a, b, A, B) indicate significant differences between K_{DL} means ($p \leq 0.05$).

Source of variance		K_{DL} range (mg 100 g^{-1})	K_{DL} mean (mg 100 g^{-1})	Δ K_{DL} stocks (kg^{-1} ha^{-1})
Rewetting time	0 years (1999)	16.9–77.5	29.8 b	
	4 years (2003)	18.5–84.4	34.3 b	11
	6 years (2005)	7.9–50.1	17.9 a	-69
	17 years (2016)	9.1–51.3	30.1 b	38
Grassland management	Meadow	10.6–39.6	24.4 A	
	Mixed use	7.9–77.5	30.3 B	
	Pasture	7.9–84.4	29.3 B	

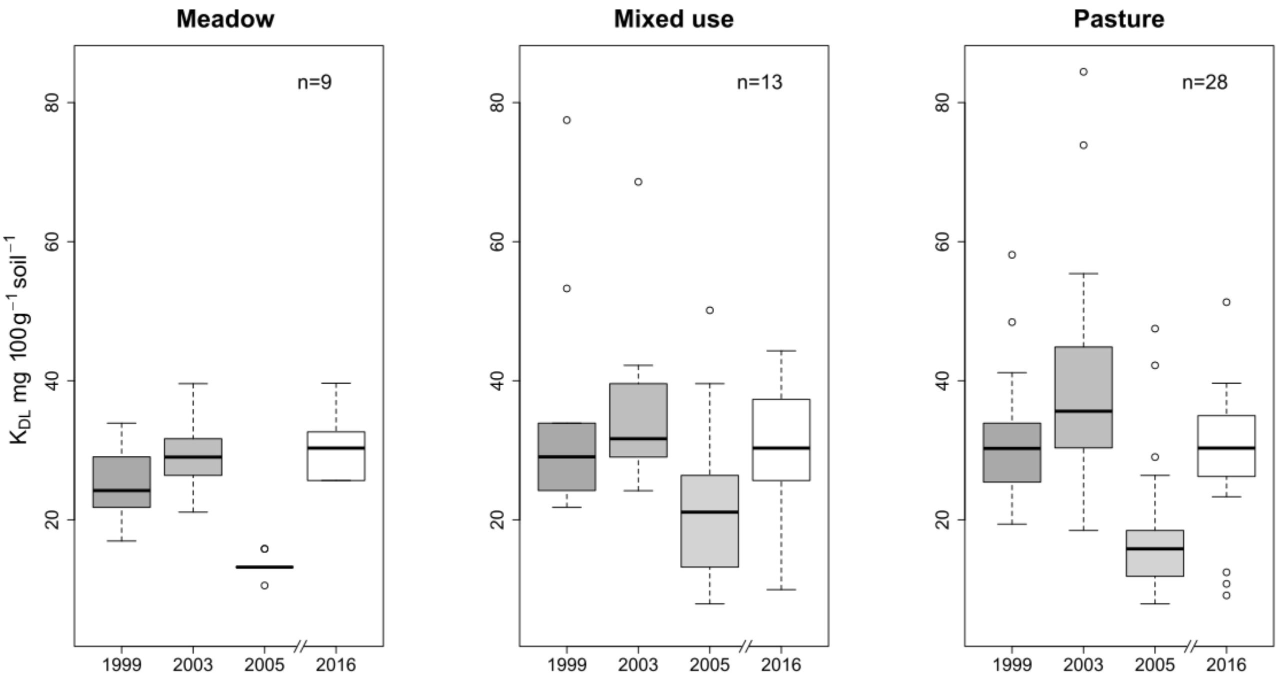

Figure 4. Dynamics of K_{DL} content (0–10 cm) for the three types of grassland management (box plots are marked by the first and third quartile, the median divides the box, the whiskers represent observations outside the 9–91 percentile range, and values falling outside the range are dot-plotted as outliers).

the K_{DL} values on the pasture fields were in the range of the initial K_{DL} content. The lowest initial K_{DL} values of 24.8 mg 100 g^{-1} were found in 1999 on the meadow fields (Figure 4). In the first four years, the mean K_{DL} content increased by 16 %, and then up to 2005 the K_{DL} content decreased by 53 % on average and showed the lowest values of all grassland treatments. In the long term, the K_{DL} content increased and clearly exceeded the initial values. The mean K_{DL} content of the mixed-use type amounted to 33.5 mg 100 g^{-1} in the first survey year and also increased in the first four years by 4 % (Figure 4). In the following two years, the mean K_{DL} content decreased by 35 % below the initial 1999 value. After 17 years of cutting and grazing, the K_{DL} content was back to its 1999 level. In all survey years the mean K_{DL} values of the mixed-use type were above the pasture and meadow management types. In the first three survey years, the mean K_{DL} values of the pasture fields were 3.9 to 10.6 mg 100 g^{-1} above the meadow type. Despite slight differences in the K_{DL} values in the first survey year and differences in nutrient export, the K_{DL} contents of the three grassland management types were within a narrow range of 29.5 and 30.6 mg 100 g^{-1} in the last survey year.

Effects of soil ash content and pH value on K_{DL}

The peat ash contents of all the fields were within a wide range of 16 to 80 %, with an average across all fields of 32 ± 12 %. Only three field samples showed a peat ash content greater than 60% (Figure 5). Ash content was significantly negatively correlated with K_{DL} content, with a correlation coefficient of -0.48 ($p <0.00$; Pearson's-k; t = -3.837, df = 48). According to the regression analyses, about 23 % of the variance in K_{DL} can be explained by the ash content of the peat (Figure 5).

Over the survey period, soil pH values were consistent and within a range of 4.9 and 5.0, with grassland management and differing water levels producing no changes in pH values. An overview of the annual pH values related to grassland management and WTD is given in Table 5.

DISCUSSION

General status and dynamic of K_{DL}

Despite the fact that the extensive grassland management did not involve the application of fertiliser, the K_{DL} content was surprisingly high. After 17 years of seasonal rewetting during winter, the mean K_{DL} content (30.1 mg 100 g^{-1}) even slightly exceeded the K_{DL} content of the first survey year (29.8 mg 100 g^{-1}). From an agricultural perspective, the K_{DL} content was still within the range required for an appropriate K supply of Histosols (20 to 34 mg 100 g^{-1}; LUFA Nord-West 2017; assumed bulk density: 0.365 g cm^{-3}; no distinction between fen or bog peat substrate). However, the K_{DL} content varied

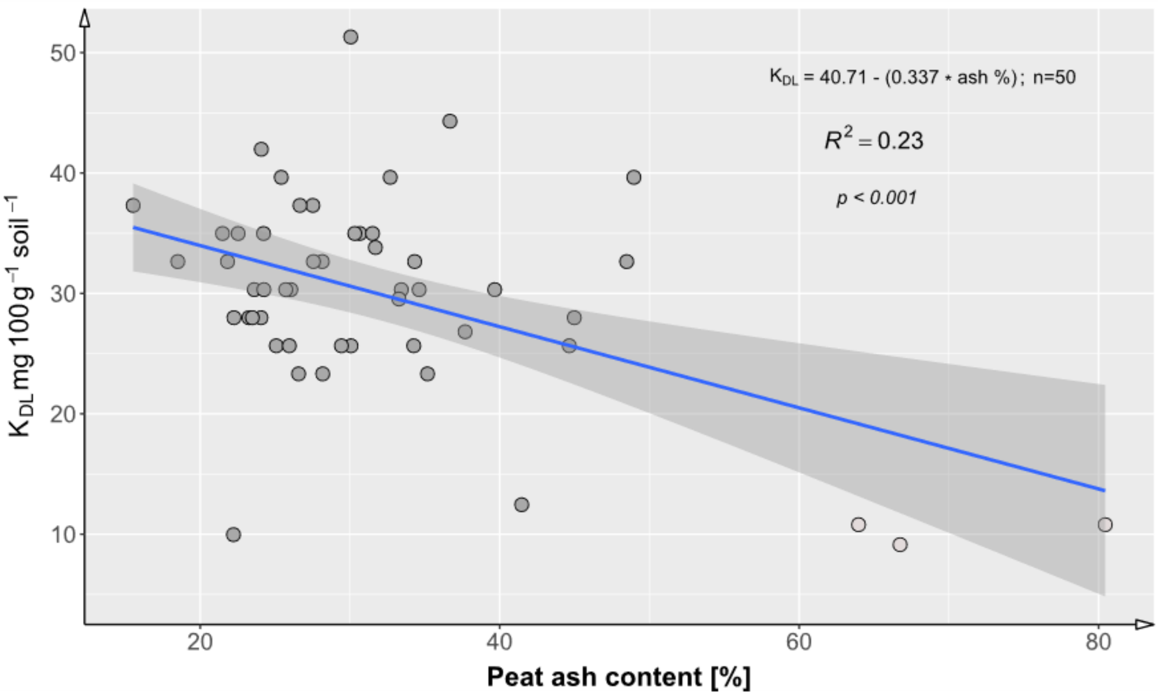

Figure 5. Relationship between peat ash content and K_{DL} (n = 50). The blue line indicates the trend and the 95 % confidence interval is given by the grey corridor.

Table 5. The pH values of the topsoil (0–10 cm) by survey year and type of grassland management (mean ± standard deviation).

Grassland management	1999	2003	2005	2016
Meadow (n = 9)	5.0 ± 0.3	4.9 ± 0.2	5.0 ± 0.3	5.0 ± 0.2
Pasture (n = 28)	4.9 ± 0.2	4.9 ± 0.2	4.9 ± 0.3	5.0 ± 0.2
Mixed (n = 12)	4.9 ± 0.2	4.9 ± 0.2	4.9 ± 0.2	4.9 ± 0.2

substantially over the years. In 2005 in particular, the K_{DL} content was not sufficient, from an agricultural point of view, for an adequate K supply of the grassland in 66 % of the study fields.

Short-term studies (one to seven years) on Histosols with water tables below the surface and extensive grassland management show a relatively low K_{DL} ranging from 4.1 to 9.5 mg 100 g^{-1} (Eschner & Liste 1995, de Mars *et al.* 1996, Koppisch *et al.* 2001). Even in clay-rich Histosols with a higher K-binding capacity, the K availability is within the same K_{DL} range (Oomes *et al.* 1996). In contrast to these earlier findings, the annual mean K_{DL} contents of 17.9 to 30.1 mg 100 g^{-1} in the Osterfeiner Moor seemed to be exceptionally high. This was particularly surprising because previous studies have recorded a rapid decline in the plant-available K stock within 10 years due to a permanent nutrient offtake with annual hay removal (Oomes *et al.* 1996, van Duren & van Andel 1997, Benke & Isselstein 2001, Olde Venterink *et al.* 2002b, Oelmann *et al.* 2009, Olde Venterink *et al.* 2009). However, high K_{DL} values of up to 17 and 50 mg 100 g^{-1}, which are comparable with the results of the present study, have been found in Histosols with high water tables and very extensive grassland management or in pristine fens (de Mars *et al.* 1996, Koppisch *et al.* 2001). Some authors point out that continuous inundations clearly increase the plant-available K stock (de Mars *et al.* 1996, Koppisch *et al.* 2001, Oelmann *et al.* 2009, van de Riet *et al.* 2010) or that K becomes less deficient compared with drained conditions (van Duren & van Andel 1997). Similarly, a lateral inflow of K-enriched surface water in the Osterfeiner Moor can be assumed (see also “External sources of K in the study area” below). Flooding events in the study area with water levels above the ground surface (WTD + 20 cm) coincided with increased K_{DL} values in the sampling years 2002, 2003 and 2016. Only in 2005 was the K_{DL} content significantly lower on all types of grassland management. This temporary depletion might be explained by large vegetation production accompanied by an increased plant uptake of K (there was no opportunity to record the biomass offtake), as well as by the absence of K inflow by surface water. During the sampling years 2003 to 2005, water levels did not exceed the topsoil horizon due to much lower rainfall rates compared with the long-term average. Additionally, the occurrence of free drainage conditions during that time may have promoted increased K leaching from topsoil. Koerselman & Verhoeven (1992) and Mundel (1992) report substantial K losses with leaching rates of -10 to -18 kg ha^{-1} a^{-1} per 100 mm percolation water. Based on the groundwater recharge rate, the mean K leaching in the present study area may have been -18.2 to -32.8 kg ha^{-1} a^{-1} (according to the climatic water balance from November 2003 to October 2005: 182.1 mm) and at least partly contributed to the K_{DL} stock changes of -69 kg ha^{-1}. However, further investigations of K pathways are needed to clarify the leaching behaviour and uptake by vegetation under permanently changing water levels.

External sources of K in the study area

Generally, there are three external sources for K input to unfertilised peatlands: atmospheric deposition, groundwater inflow and flooding events (Koppisch *et al.* 2001). Goulding *et al.* (1986) and OldeVenterink *et al.* (2002b) report that annual atmospheric deposition rates usually amount to no more than 1.9 to 5 kg ha^{-1} a^{-1}. Deposition rates in this range are too small to be of relevance for plant nutrition or to have an effect on soil K stocks. Inflow of nutrient-enriched groundwater with a rise in the water table is another possible input of K (Koerselman & Verhoeven 1992). However, in the present study area, the shallow peat layer is underlain by thick, almost impermeable algal gyttja (Pfaffenberg & Dienemann 1964, Blankenburg *et al.* 2001) with a saturated hydraulic conductivity of 0.5 cm d^{-1} (Blankenburg & Hettwer 2006). It is therefore unlikely that the topsoil K stock was affected by groundwater inflow from deeper K-bearing sediments. The third possible source of K input is flooding events. Olde Venterink *et al.* (2002b) and Koppisch *et al.* (2001) state that K input in peatland is mainly supplied by surface water. The K input by flooding events has been reported to amount to 21 to 28 kg ha^{-1} a^{-1} (Koerselman & Verhoeven 1992, Olde Venterink *et al*. 2002b). The changes in K_{DL} stocks of 11 and 38 kg ha^{-1} were within a range that could be explained by K input from flooding, and coincide with high water levels (2001/02, 2002/03 and 2015/16). Therefore, induced flooding events may play a critical role in the redistribution of nutrients in Histosols and in the maintenance of soil fertility.

Effects of grassland management on K_{DL} dynamic

Despite a strong impact of the hydrological conditions on K dynamics, grassland use also affects absolute K_{DL} content. In the first years after the restoration measures were implemented, K_{DL} means differed significantly between the type of grassland management. The meadow fields in particular showed lower K_{DL} contents than pastures and mixed-use fields. This is in agreement with other wet grassland studies. Extensive biomass removal (1–2 hay cuttings per year) can considerably decrease the plant-available K content in unfertilised meadows by 15–73 kg ha^{-1} a^{-1} (Koerselman *et al.* 1990a, Benke & Isselstein 2001, Olde Venterink *et al.* 2002b, Oelmann *et al.* 2009, van de Riet *et al.* 2010). Therefore, the decrease in the K_{DL} stock by -69 kg ha^{-1} in the sampling years 2003 and 2005 could at least partially have been caused by biomass export.

In contrast, the higher K_{DL} values in pasture fields can be explained by an absence of nutrient offtake with hay biomass, and particularly by the internal cycling of K in pasture with a comparably small uptake of K in livestock (Kayser & Isselstein 2005). In pasture-based grassland systems, 90 % of ingested K returns via excrement back to the soil K pool (Hutton *et al.* 2012, Weil & Brady 2017). In an intensively managed pasture system, annual K recycling can amount to up to 120 kg ha^{-1} (Käding 1994). The redistribution of K by cattle excrements may explain the higher K_{DL} stocks (+ 16.1 to 43.4 kg ha^{-1}) compared to the meadow management type, within the first three survey years. Furthermore, the pasture fields had the largest between-field variance compared with meadows or mixed use. This is attributed to the effect of a spatially uneven nutrient return with urine and faeces (Kayser & Isselstein 2005).

K_{DL} values in the mixed-use fields, which are characterised by a first cut followed by grazing of the regrowth, did not differ from the values found in the pasture system. Values between those for meadow and pasture were expected. It appears that in addition to the return of K with animal excretions, other processes must have contributed to balancing the K offtake with the first cut. However, these grassland management effects were found to be less pronounced overall the longer the restoration period continued. In the final sampling year, K_{DL} content did not differ between the grassland management types.

Effect of peat degradation, mineral content and pH on K_{DL}

The Osterfeiner Moor has been subject to intensive drainage and agriculture in the past century. This intensive cultivation transformed the Holocene sedge peat to a strongly amorphous peat. The increased ash content and very high von Post values were in agreement with previous soil surveys in the Osterfeiner Moor area (Blankenburg *et al.* 2001). Despite ongoing seasonal rewetting measures, the peat decomposition processes continued to an extent. The degree of decomposition expressed by the peat ash content had a significant effect on changes in soil nutrients and explained a maximum of 23 % of the variability in K_{DL} content. Particularly in three fields with a peat ash content above 60 %, ongoing decomposition processes may affect K_{DL} dynamics. However, most of the topsoil samples had a peat ash content well below 50 %. It was assumed that peat ash decomposition only had a very small effect on K_{DL} content here.

High ash contents are also an indicator of an enrichment of mineral constituents due to sedimentation processes during or after peat formation as well as ongoing peat mineralisation (Krüger *et al.* 2015). The negative correlation between K_{DL} and ash content suggested that the incorporated mineral constituents had no positive effect on K-binding capacity. Accordingly, K-bearing or specifically K-binding minerals were absent or had already dissolved (e.g. micas, feldspars). It was assumed that weak K binding is mainly enabled by the less specific surface negative charge from functional groups of the organic soil constituents.

This finding led to two assumptions about the interpretation of the strong K dynamics over the sampling years. First, the unspecific weakly adsorbed monovalent K^+-ions are easily displaced by other cations and vulnerable to translocation under a changing water regime. Second, the CEC of peat is predominantly attributed to the variable charge of mainly carboxylic and phenolic groups. The charge of both functional groups is, in turn, pH dependent (Brown *et al.* 2000, Kyziol 2002). Therefore, changes in pH value may modify the adsorption-desorption behaviour of SOM and vice versa (Ma & Tobin 2004). However, the pH values in the study area were very stable and only ranged between 4.9 and 5.0 (± 0.2). Such small differences cannot explain the great changes in K_{DL} content over the years.

CONCLUSIONS

This long-term survey of restored wet grasslands over a 17-year period showed that K recharge from periodical flooding events balanced K_{DL} and attenuated grassland-specific K losses. Biomass removal from meadows and the internal cycling of nutrients on pastures with the return of excrement clearly affected the K_{DL} content in topsoil only in the early years. These grassland management effects became less important over time due to K input from flooding events. In years when water tables are below the topsoil, K_{DL} content can decrease in a relatively short time. Particularly in prolonged drought periods, K_{DL} content should be regularly monitored to ensure sustainable nutrient management and sufficient biomass production. The effect of peat degradation on K_{DL} content was negligible. Further studies are needed to understand the long-term effects of rewetting measures and grassland management on nutrient export, K cycling in extensive pasture systems and the amount of K input from adjacent water bodies or regular flooding events.

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AUTHOR CONTRIBUTIONS

JM initiated the project and designed the study. SH wrote the first draft of the manuscript and conducted the study together with JM and MK. The Figures and Tables were prepared by SH and JM. All of the hydrological data, including modelling of water tables, were provided by SJ and subsequently summarised by SH. SH, JM and MK analysed all of the given data. MK, JM and SH revised the final version of the manuscript.

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