



Research article

Plant functional type and peat properties determine elemental transfer in boreal mire vegetation

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ABSTRACT

Uptake of elements into plants is an integral part of many environmental impact assessments. Typically, the plant uptake is determined using an empirical soil-to-plant transfer factor (CR). The elemental concentrations in plants are expected to vary with plant species and plant functional type (PFT), but also according to soil and element properties. Specifically, the uptake of essential elements is regulated, and likely less related to soil concentrations than the uptake of non-essential elements. In this study, the impact of PFT, species and environmental factors on the CR of mire plants was tested. The plants included in the study were four common boreal peatland species (*Andromeda polifolia*, *Vaccinium oxycoccus*, *Eriophorum vaginatum* and *Carex rostrata*) sampled from 40 minerogenic mires along an age gradient.

The results show that while plant species and PFT (heathers and sedges) are the main determinants of the CR value, also environmental factors, such as peat C:N ratio, are important. Further, concentrations of essential elements in plants were only weakly correlated to peat concentrations, whereas the correlation was stronger for non-essential elements and elements utilized at trace amounts.

The results of this study verify that CR values may vary substantially between peatland plant species and PFTs. Further, the results suggest that it is relevant to include effects of PFTs on CR and among-species variation in environmental impact assessments. This is because the PFT may have a large impact on the exposure pathways to humans, which could, for example, be berries or animal feed, and also due to the uncertainties of the composition of the future vegetation communities. Since CR varies systematically with several soil properties, there may be potential for adjusting the CR values for expected environmental changes, and thereby reduce the uncertainties of empirical CR values determined from a broad range of environmental conditions.

1. INTRODUCTION

Environmental impact assessments are used to estimate the environmental consequences of a plan, policy, program, or project with possible impacts to the surrounding environment, and are typically required by national or international authorities before any actions may be taken. For example, this kind of assessment is mandatory prior to a construction of any type of waste management facility. All potential future impacts of such facility are assessed and predicted using various modelling approaches, which require data from the

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site describing both, the chemical and biological site characteristics. These models describe transport and accumulation of contaminants in the environment, and are used to assess exposure to humans and other organisms living in the affected areas. The reliability of such models depends on high quality data that can be applied to represent element transfer under relevant environmental conditions [1,2]. The time frame of the assessment depends on the type of the facility, and may stretch even up to one million years in the future in a case of a repository for radioactive waste [3,4]. Possible leakages from a repository to the groundwater are often eventually discharged to low points in the landscape, and are likely to reach lakes, streams and mires in the future terrestrial environments [4,5]. Thus, the contaminants entering the surface ecosystems may accumulate in sediments and peat, and eventually enter the terrestrial food chain ending up in organisms that may be hunted and harvested by human inhabitants. Moreover, if the future land-use involves cultivation of drained mires, the contaminants may end up in crops, livestock meat and dairy products [6].

Uptake of elements into plants is, thus, a key process for several relevant exposure pathways. Although mechanistic soil-to-plant transfer models have been advocated by some authors [7,8], empirical soil-to-plant transfer factors, also referred to as *concentration ratios* ($CR_{\text{plant-soil}}$), are the most common way to describe plant uptake in environmental impact assessments of heavy metal and radionuclide contaminants [9,10]. The CR approach is implemented, for example, in the widely used RESRAD-BIOTA code [11] and the ERICA tool [12]. In general, there is a lot of interest on soil-to-plant transfer for hazardous elements. A large part of this literature is focused on agricultural crops [7,13–16], specific radionuclides and/or heavy metals (such as ^{137}Cs , ^{210}Pb and ^{238}U) [13,14,17–19], contaminated conditions [17,20–23] and phytoremediation [21,24,25]. Studies of non-hazardous elements and soil-to-plant transfer in natural conditions is more limited.

Overall, the observed relationships between element concentrations in plants and environmental concentrations have been shown to vary extensively. Factors that affect this variability include plant properties (for example, growth, transpiration rate and root distribution) and the availability of an element for uptake, which in return depends on, for example, chemical speciation and mobility [26]. Consequently, to reduce variability and increase precision in models predicting plant uptake, CR values are typically determined separately for different plant functional types (PFT), soil types, ecosystems, climatic conditions and often even sites [2,27]. Although not as commonly applied, soil chemical properties (such as, organic matter content and pH) have also been used to describe systematic variation in CR. This potentially yields estimates of plant uptake that account for the element availability that is dependent on soil conditions [28]. The relationship between plant and soil concentration can also be expected to vary with the nutritional value of the element for the plant. That is, patterns of essential elements subject to regulated plant uptake are not expected to be the same as for non-essential elements with no or limited biological function. If there is a linear relationship between the concentrations in plants and soil (and concentrations in plants are negligible at low soil concentrations), a general CR value will yield an unbiased estimate of uptake along the full range of soil concentrations [29,30]. However, non-linearity between plant uptake rates and soil concentrations of many elements is well documented in studies on essential plant nutrients [31], heavy metals [32,33] and elements relevant for radioactive waste [34]. Thus, describing the response of elemental plant concentrations as a non-linear function of soil concentrations has the potential to capture better the observed relationship between plant and soil concentrations. Further, studies addressing the transfer factors for a wider variety of plants, elements and environmental conditions are needed in order to capture different future scenarios for environmental impact assessments.

This study investigates the soil-to-plant transfer of 19 elements in four mire plants (*Andromeda polifolia*, *Vaccinium oxycoccus*, *Eriophorum vaginatum* and *Carex rostrata*). The elements were chosen based on their relevance for plant growth and/or environmental impact assessment of geological repositories for nuclear waste. As the concentrations of radionuclides typically are low in the environment, stable isotopes of the same elements were used. This is a common practise in radioecological modelling [35,36]. The mires are located in Northern Sweden, in the area which is subject to isostatic rebound since the last deglaciation, with a current rate of ca 9 mm yr⁻¹ [37]. In this postglacial landscape, the elevation above sea level reflects a chronological sequence of time elapsed since the land emergence from the sea. Hence, given similar climate and geological settings within a constrained distance from the coast, it is possible to study long-term ecosystem development [38]. In the present study, forty mires were used. These mires are located along two transects, which span almost 5000 years of age within only 15 km from the coast. From this data, plant to soil concentration ratios were estimated using a power function to describe the plant response, and identify sources of systematic and random variation in the CRs. The selected elements represent plant macro- and micronutrients and/or stable analogues of radionuclides. The aim of this study was to examine how the concentrations in plants depend on elemental concentrations in peat, and to discuss what implications these results have for modelling plant uptake in environmental impact assessments stretching in the far future.

2. MATERIALS AND METHODS

2.1. SITE DESCRIPTION

Post-glacial land uplift in northern Sweden along the Gulf of Bothnia has created a landscape with high peatland abundance along an age gradient spanning approximately 5000 years within 15 km from the sea [38]. The age of mire initiation along this gradient in the Sövar Rising Coastline Mire Chronosequence (SMC) was estimated according to a local shoreline displacement curve for southern Västerbotten [39]. The topographic relief of the area is limited, and the groundwater table in the mires is on average located at an approximate depth of 0–20 cm, with a mean annual variation around 10 cm [40]. The low topographic relief and the high groundwater levels are indicative of a superficial flow system with little regional influence. In this landscape, land uplift creates the conditions for peat to form on what used to be the seabed. As the mire grows vertically, the surface peat successively separates from the underlying sources of minerogenic elements, and minerogenic inputs from the adjacent upland catchments become more important. All mires included in the study are minerogenic mires (fens) [41]. However, also the contribution of the surrounding mineral soil catchment [42]

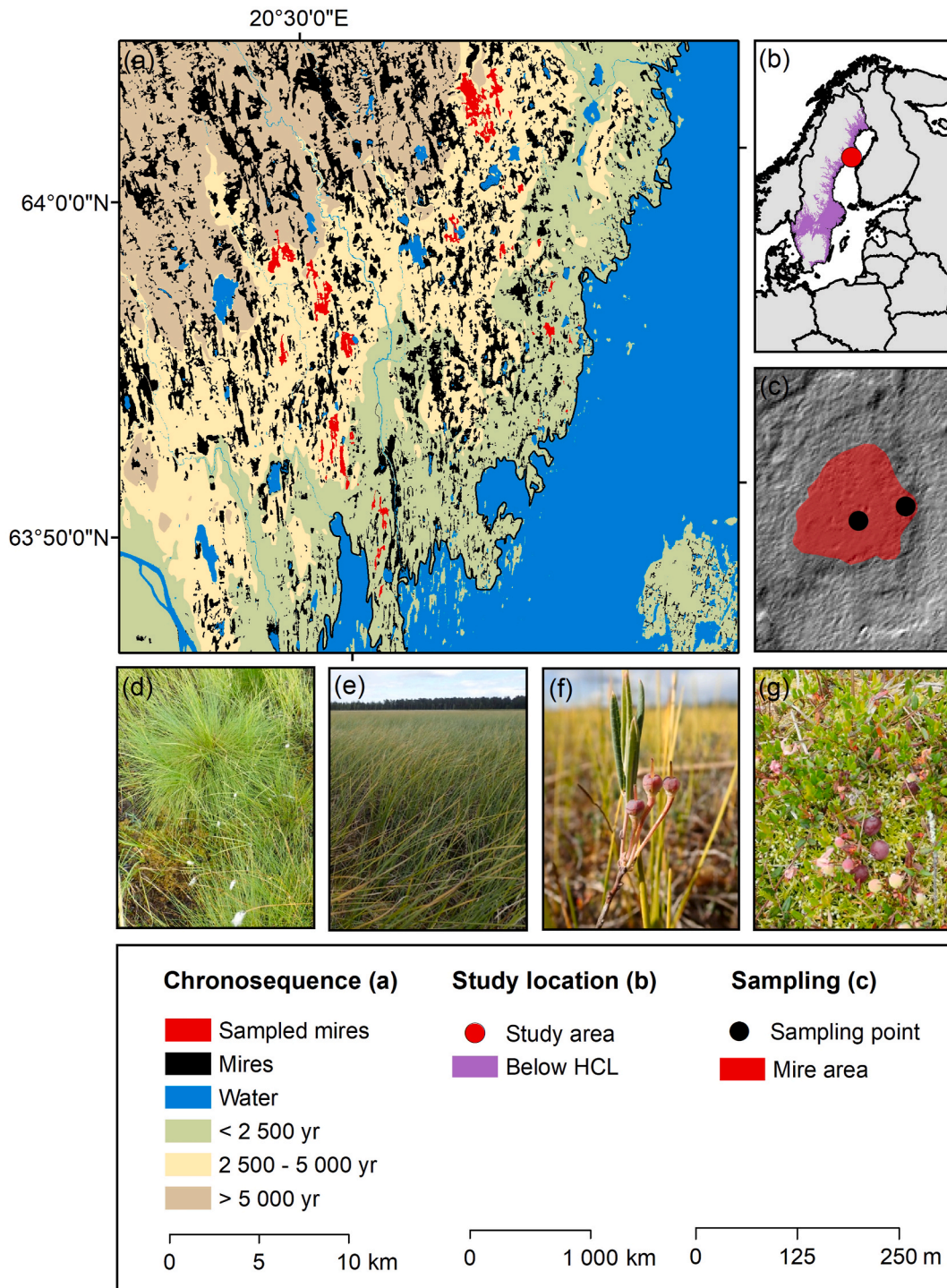


Fig. 1. Map of the sampled chronosequence mires and the sampled plants. A) The locations of the sampled mires in the Sävär Rising Coastline Mire Chronosequence. The background colours represent the approximate age of the mires in the area. B) The location of SRC. C) Locations of the sampling points at the mires. The red color represents the total mire area and black dots are the sampling location at the edge and middle of the mire. The plants sampled from the mires include D) *Eriophorum vaginatum*, E) *Carex rostrata*, F) *Andromeda polifolia* and G) *Vaccinium oxycoccus*. D) and E) represent sedges, while F) and G) are the heathers. HCL= Highest coast line. Photos: Betty Ehnvall.

to element concentrations changes substantially with time due to weathering of the surface soil minerals [43].

2.2. PEAT AND PLANT SAMPLING

Forty mires along two transects separated by the Sävar river were sampled (Fig. 1a and b, Table 1). The selected mires were evenly distributed along the age gradient, and also represented mires with different sizes. Furthermore, no ditches visible from aerial photographs or from a 2×2 m digital elevation model from Lantmäteriet (<https://www.lantmateriet.se/en/geodata/geodata-products/product-list/elevation-model-download/>) crossed the mire surface within <50 m from the sampling points, which excludes the influence of drainage on surface peat properties [44]. At each mire, pairs of edge and mid points were sampled at random order between 2nd July and August 30, 2018. Most edge points were placed 10 m from the mire edges, while in some of the smallest mires the edge points were placed 5 m from the mire edge due to short distance across the mire surface. The mid points were placed at the centre of the mire expanse, directly out from the edge sampling points (Fig. 1c). The mire edges were identified in the field based on the vegetation and peat depth. All sampling points were mapped using a Trimble GeoExplorer 6000 GPS with a vertical and horizontal precision of 0.02 m. Photos from the sampled mires are provided in the interactive mire chronosequence map (<https://slughg.github.io/MiresChrono>). Surface peat samples for measuring elemental concentrations and dry bulk density (BD) were collected from each sampling point by cutting a 6×6 cm wide and 10 cm deep peat sample using a knife with a stainless-steel blade. The living vegetation was identified visually and peat below was sampled. A separate sample was collected from the same sampling depth for measuring electrical conductivity (EC) and pH. The total peat depth was measured at each transect point by pushing a metal rod into the peat until it reached a non-penetrating surface. All peat and plant samples were stored in plastic bags and placed in a freezer (-18°C) within 8 h after extraction.

Four plant species that were expected to be abundant across the mire transect, both in terms of age and nutrient gradients, were included in the study, and sampled when present at the sampling points. These were *Andromeda polifolia* (L.) (AP; N = 64), *Vaccinium oxycoccus* (L.) (VO; N = 20), *Eriophorum vaginatum* (L.) (EV; N = 58) and *Carex rostrata* (Stokes) (CRo; N = 16). Of these, AP and VO are members of the Ericaceae family and are here considered heathers, whereas EV and CRo belong to the family Cyperaceae and are here representing sedges.

Andromeda polifolia (bog-rosemary) is a native species of flowering plants, found in cold peat-accumulating areas of the Northern Hemisphere. It is a 10–20 cm tall evergreen shrub with slender stems. It has a large root system that may reach up to half a meter depth and be 2 m wide, with ericoid mycorrhiza associated to it [45].

Vaccinium oxycoccus (cranberry) is about 10 cm tall flowering plant in the heather family. It is widespread and common species occurring broadly across cooler climates in the boreal and temperate northern hemisphere. It is typically found at minerogenic (fens) and ombrogenic (bogs) mires, which are low in nitrogen and have a high water table. It is a small, prostrate shrub with vine-like stems that root at the nodes and leathery, up to 1 cm long lance-shaped leaves. Flowers arise on nodding stalks. The fruit is a red berry, which ripens late in the autumn. It mainly reproduces vegetatively. The plant forms associations with ericoid mycorrhizae [46].

Carex rostrata (bottle sedge or beaked sedge) is a 30–100 cm tall perennial species of sedge in the family Cyperaceae. It is typically found on fens with a high water table. The flowers have separate staminate (male) and pistillate (female) spikes. It has basal and alternate leaves, which are 1.5–4.5 mm wide. Fruits develop in late spring to mid-summer. The plant has no mycorrhizal associations [45].

Eriophorum vaginatum (hare's-tail cottongrass, tussock cottongrass, or sheathed cottongsedge) is a species of perennial herbaceous flowering plants in the sedge family Cyperaceae. It is native to bogs, poor fens, and other acidic wetlands. It is a 30–60 cm high tussock-forming plant with solitary spikes and narrow hair-like leaves. The flowering stems have a single, inflated leaf-sheath without a lamina. The inflorescence is a dense, tufted, solitary spike. Fruiting stems elongate considerably, reaching well above the leaves. The plant has no mycorrhiza [45].

In total 158 plant samples from 80 sampling points were included in the study. For the majority of sampling points (60 out of 80) two different species were collected, representing both heather (AP, VO) and sedge (EV, CRo) type of vegetation. At 14 sampling points

Table 1

Description of the sampled mires along two chronosequences at the Swedish coast. Each mire was sampled at two locations, in the centre of the mire and at the edge. Peat properties are listed for each of the two strata.

Location/properties	Position	N	Mean	Std Dev	Min	Max
Northing		80	7098654	7956	7085997	7114053
Easting		80	775782	5218	767141	783680
Elevation (m.a.s.)		80	24	17	2	58
Peat depth (cm)	Edge	40	59	32	21	156
	Centre	40	124	82	22	300
Bulk density ($\text{kg}_{\text{dw}} \text{dm}^{-3}$)	Edge	40	0.045	0.014	0.005	0.072
	Centre	40	0.040	0.013	0.006	0.066
pH	Edge	40	4.28	0.29	3.75	4.97
	Centre	40	4.29	0.29	3.78	4.95
Electrical conductivity ($\mu\text{S cm}^{-1}$)	Edge	40	68.3	30.0	27.6	145.4
	Centre	40	49.2	17.2	21.4	99.9
C/N ratio	Edge	40	63	17	29	94
	Centre	40	71	24	32	124

(in seven mires) only one plant species was present, whereas all four species were present at six sampling points (in three mires).

2.3. CHEMICAL AND PHYSICAL ANALYSES

The concentrations of 19 elements in plant and peat samples were analysed in this study. These elements included five macronutrients (Ca, K, Mg, S, P), seven micronutrients (B, Cu, Fe, Mn, Mo, Ni, Zn; [47]), and seven non-essential elements that are relevant with respect to the safety of geological repositories of radioactive waste (Ba, Cs, I, Pb, Sr, Th, U). Moreover, several of the included plant nutrients also have radioisotopes that are highly relevant for assessing environmental impacts (in particular, Ca, Mo and Ni).

Prior to elemental analysis, the peat and plant samples were oven dried at 60 °C for three days, and larger roots (diameter >1 mm) were removed from the peat samples. The roots *per se* were not analysed in this study, only the above ground plant parts. Ground and homogenized samples (0.5 g) were then digested with aqua regia for 2 h in a heating block at 90 °C. Leachates were diluted and analysed for elemental concentrations using Inductively Coupled Plasma Sector Field Mass Spectrometry (ICP-SFMS) with methane addition, and analytical background concentrations were subtracted from measurements.

Peat bulk density was determined gravimetrically. Porewater conductivity (EC) (INESA DDS-307, INESA & Scientific Instruments Co., Shanghai, China) and pH (Greisinger GMH5530, GHM Messtechnik GmbH, Standorf Greisinger, Germany) were measured at 20 °C from peat slurries. For this, 50 ml Milli-Q water was added to equivalent of 2 g dry peat, shaken for 15 min and left to equilibrate overnight before measurement.

2.4. STATISTICAL ANALYSES

When the CR concept is used, the steady-state radionuclide concentration in plants ($Conc_{plant}^m$) is calculated as being proportional to the concentration of radionuclides in the soil ($Conc_{soil}^m$) (Eq. (1)). For radionuclides that have stable isotopes in the environment, the CR value is typically estimated from the ratio of the elemental concentrations of stable isotopes between the plant ($Conc_{plant}^e$) and soil ($Conc_{soil}^e$). As radionuclides are expected to occur in concentrations far below background levels of stable isotopes, the CR concept can be seen as a specific activity approach (right hand term Eq. (1)), i.e. the radionuclide concentration in plants is derived from the specific activity in soil and the elemental concentration in the plant:

$$Conc_{plant}^m = CR_{plant-soil} \cdot Conc_{soil}^m = \frac{Conc_{plant}^e}{Conc_{soil}^e} \cdot Conc_{soil}^m = \left(\frac{Conc_{soil}^m}{Conc_{soil}^e} \right) \cdot Conc_{plant}^e \quad (\text{Eq. 1})$$

In this study, the response of plant uptake to soil concentrations is also described using a power function, which yields the following expression for the $Conc_{plant}$ and $CR_{plant-soil}$:

$$Conc_{plant} = 10^a \cdot (Conc_{soil})^b \quad (\text{Eq. 2})$$

$$CR_{plant-soil} = 10^a \cdot (Conc_{soil})^{b-1} \quad (\text{Eq. 3})$$

The constant 10^a is the expected plant concentration given a soil concentration of one unit. The constant b describes the strength in the response. The values of a and b can be determined from a linear regression of plant concentration as a function of soil concentrations on log-log scales. In the specific cases where b equals 1, plant concentrations are proportional to soil concentrations and $CR_{plant-soil}$ is independent of soil concentrations (as traditionally assumed). When b is between 1 and 0, $CR_{plant-soil}$ will show a non-linear response and CR will decrease with increasing soil concentration (the exponent in eq. (3) is negative). In the case where b equals 0, plant concentration is independent of soil concentration and under such conditions, it would be more intuitive and straightforward to predict radionuclide uptake from the average plant element concentrations and the specific activity of the radionuclides in soil [48].

The correlation patterns of the concentrations of elements in plants and peat samples were examined with principal component analysis (PCA), and the scores along the first two principal components were used as derived variables in the subsequent analysis. Interaction tests of significance were determined from F-ratios. For the analysis of PC score, the factor sample type (Peat, Plant) was included as an additional fixed factor. Mire and sampling point (within a mire) were treated as random factors. For the final estimates of CR variation, species (within PFT) was also treated as a random factor.

Plant and peat concentrations, and the ratio of these two, were log transformed prior to all analyses. Thus, the mean values (and standard errors) were calculated on a logarithmic scale, and back-transformed for the presentation of results (corresponding to the geometric mean and the geometric standard deviation). Residuals were approximately normally distributed and independent of fitted values. All statistical analyses were carried out with JMP®, Version 17 (SAS Institute Inc., Cary, NC, 1989–2023).

The effects of environmental factors on CR were examined with a multiple regression approach using elevation (m) (a proxy for the age of a mire), peat depth (m), bulk density ($kg_{dw} dm^{-3}$), peat C:N ratio, pH and electrical conductivity ($\mu S cm^{-1}$) as regressors. The variance inflation factors of the regressors were 1.9 (C:N ratio) or lower, indicating an acceptable level of multicollinearity [49]. The effects of PFT and species (within type) were also included in the model as class variables. T-values were used to determine significance of individual regressors. The element concentrations in plants and peat were analysed with the same regressors to examine whether the CR response was due to a change in the concentration in the plant, the peat or both.

The response of concentrations in plants to variation in the concentrations in peat, was studied with a regression approach. In this analysis, PFT and species (within vegetation type) were class variables, and peat concentration a covariate. To examine whether the

plant to peat concentration relationship depended on PFT, the response (i.e. the slope b) was estimated separately for heather and sedge, and the difference in slope was tested with the interactions between PFT and peat concentration.

3. RESULTS

3.1. OVERALL PATTERNS OF ELEMENTAL CONCENTRATIONS IN PLANTS AND PEAT

Three principal components had eigenvalues above 1, and together these explained 85 % of the total variation in elemental concentrations in plant and peat samples. The first principal component explained most of this variation (63 %) and it separated heather, sedge and peat samples from each other ($p < 0.0001$ for plant vs. peat, and for heather vs. sedge, Fig. 2a). The second component explained an additional 13 % of the variation, and separated the two different PFTs ($p < 0.0001$ for heather vs. sedge). Elements that were enriched in plant samples loaded negatively on the first component, whereas elements that occurred in relatively low concentrations in plants loaded positively on the same component. As expected, most plant macronutrients (K, P, Mg and Ca), as well as a few micronutrients (Ba, B and Mn), had negative loadings on the first component (Fig. 2a). For non-essential elements with no beneficial effects for plants (Pb, I, Th, Cs and U), the opposite was true, as they tended to have positive loadings on the first principal component. Plant species belonging to the same functional group had a similar pattern of elemental concentrations, but the patterns were clearly different between the heather and sedge species, as seen along both the first and second principal component. For example, plants of heather type had higher concentrations of alkaline earth metals (Ca, Mg, Ba) and a few micronutrients (Mn, B), whereas sedges had relatively high concentrations of most of the non-essential elements (I, Pb, Th, U). Species (within PFT) and position at the mire (edge vs. centre) did not have any significant effect on scores along the first and second principal component.

Elements with high concentration in peat also tended to have a high concentration in plants (Fig. 2b). However, the relationship

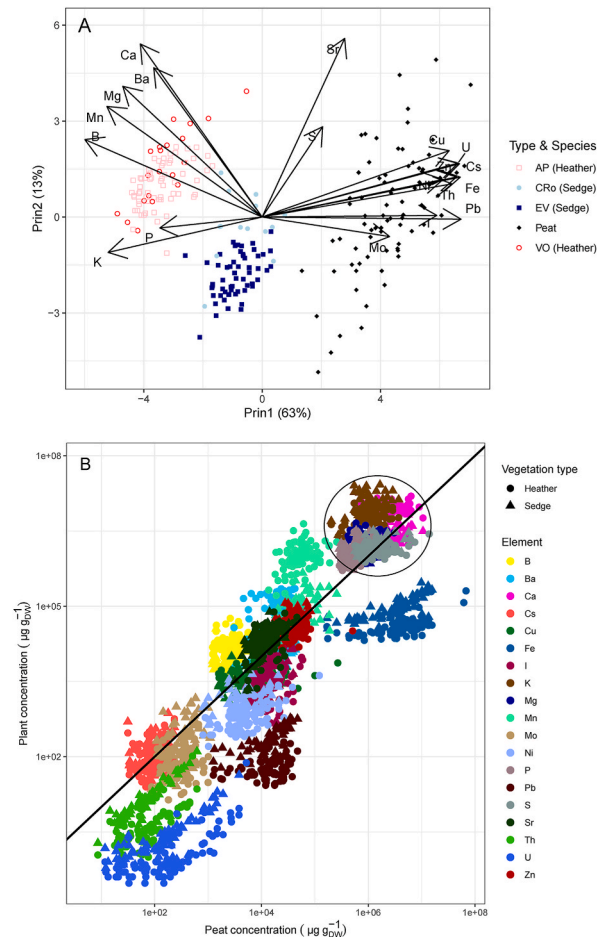


Fig. 2. Overall patterns of the concentrations of 19 elements in plants and peat sampled from 40 mires. A) A PCA plot showing the scores along the first two principal components for 160 plant and 80 peat samples. Loadings of the concentrations of individual elements are indicated by arrows. B) The concentration in plants as a function of concentration in the peat. Individual elements are indicated by colours and plant functional type by shapes. The five plant macronutrients (Ca, K, Mg, S and P) are circled. The black line represents 1:1 concentration ratio between the plants and peat.

between the concentration in plant and peat was less evident for individual elements (see section 3.4 for a detailed analysis). For macronutrients, and to a slightly smaller extent also for micronutrients, the variation in plants tended to be much smaller than the variation in peat, and the slope for individual elements was typically flatter than 1:1 (Fig. 2b). In the lower end of the concentration spectrum, non-essential elements tended to show a larger concentration variation in both plants and peat, and a positive plant-to-peat relationship was clearly evident for both U and Th. As pointed out in the principal component analysis (above), macronutrients tended to be enriched in plants (above the 1:1 line in Fig. 2b), whereas the opposite was true for non-essential elements in low concentrations. U, Pb and Fe appeared to have particularly low plant availability in the mire environment, as concentrations of these elements were significantly lower as compared to concentrations of other elements with similar peat concentrations.

3.2. EFFECTS OF PLANT FUNCTIONAL TYPE, SPECIES AND WITHIN MIRE POSITION ON CR

Plant to peat CRs for the examined elements spanned more than four orders of magnitude, with means for CR ranging from below 0.01 (U and Pb in heather) to above 10 (K in sedges) (Fig. 3). PFT was the primary source for systematic variation in CR and the difference between PFTs was highly significant ($p < 0.0001$) for all elements except for Cs ($p = 0.14$). The CR value typically differed by a factor of two or more between heather and sedge vegetation. Species differences within the PFTs were apparent for most elements ($p < 0.01$ for all elements, except for P and Mg), but the difference was typically below a factor of two. There was also a tendency for more pronounced differences in elemental concentrations between the sedge species than between the heather species; the median species difference was 60 % and 30 % for the two types, respectively. The difference in CRs between plants collected at the centre or at the edge of the mire was comparatively small (typically below 10 %). However, for a handful of elements (Fe, Cs, Cu and Ba) the CR of plants collected in the centre of the mire was consistently higher (~30 %) than for plants collected at the edge ($P < 0.05$, Table 2).

The effect of spatial distribution on the CR variation was examined for each element by partitioning the total random variation into three separate variance components, namely, variation among mires (scale of km or more), variation within mires (between sampling points; scale of ~100 m), and variation within sampling points (scale of meters). The relative importance of the three components differed markedly between elements. For example, for Cu, Fe, I, Th and U the variation between mires was the dominant source of random variation (>50 % of total variation). On the other hand, for B, Ca, K, Mg, Mn and Sr the variation between sampling points within mires was the main source of variation. Small-scale variation within sampling points was dominant for only a few elements (Ba, Cs and Mo).

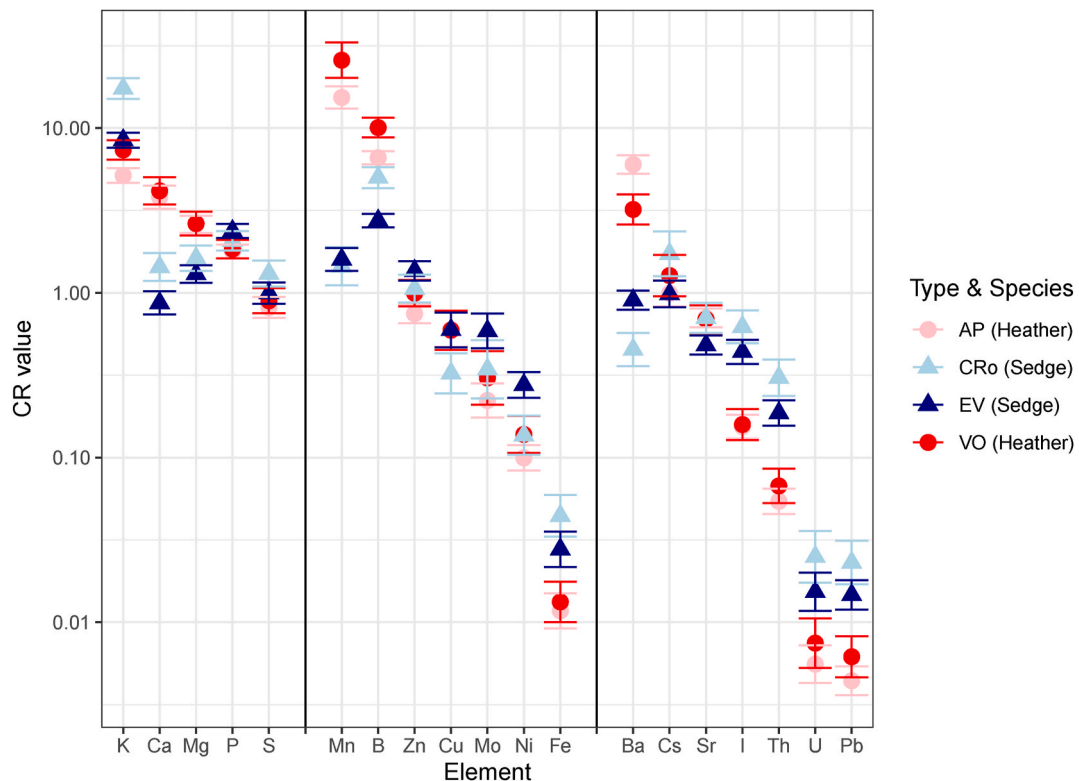


Fig. 3. Plant-to-peat concentration ratios as a function of plant species for the 19 studied elements. Elements have been grouped into macronutrients (left), micronutrients (middle) and non-essential elements (right). Geometric mean and 95 % confidence intervals are given. Vegetation type, heather or sedge, is indicated by the shape of the symbols.

Table 2

Plant-to-peat concentration ratios (CR) for 19 elements and the response in CR to changes in six environmental factors. Means and standard deviations have been back-transformed from logarithmic scale. The fold-difference in CR between the centre and edge of the mire is listed for elements with a significant difference ($p < 0.05$). The standard deviation (SD) is based on the total variance for both vegetation types. The relative response in CR was derived from a regression analysis and is expressed per listed change in each environmental factor. A relative response above 1 indicates an increase in the CR, whereas a value below 1 indicates a decrease. Listed factors are significant at the 0.05 level.

Element	Mean of PFT				Relative response (to increase)					
	Heather	Sedge	Center vs	SD	C/N	Peat depth	pH	EC	Elevation	Bulk density
	(n = 85)	(n = 75)	Edge		(50 units)	(1 m)	(1 unit)	(100 unit)	(50 m)	(0.05 unit)
B	8.1	3.7		1.7		1.11	1.27		1.31	
Ba	4.4	0.64	1.28	2.0	1.49	1.40			0.61	
Ca	4.0	1.1		1.9	1.54	1.24	0.35			
Cs	1.1	1.3	1.36	2.1		1.31		0.39		
Cu	0.60	0.44	1.28	2.4	2.17	1.16				
Fe	0.012	0.035	1.41	2.4	1.90	1.43	0.47		0.56	
I	0.16	0.51		1.8	1.87		1.54	1.70		1.75
K	6.1	12.1		1.8			1.52	0.51		1.53
Mg	2.6	1.4		1.6		1.19	0.43			
Mn	19.6	1.5		2.0		1.27			0.53	
Mo	0.26	0.46		2.5	2.41	0.80				
Ni	0.12	0.20		2.1	1.69	1.14	0.69	0.64		
P	1.8	2.2		1.5	1.68			1.34		
Pb	0.005	0.018		2.2	1.99				0.58	
S	0.85	1.1		1.7	1.95	0.85	0.58		1.35	
Sr	0.70	0.57		1.8	1.45	1.43	0.58		0.66	
Th	0.06	0.23		1.9	2.09			1.41		1.50
U	0.006	0.019		2.6	2.51	1.32				
Zn	0.9	1.2		1.7	1.20			0.75		

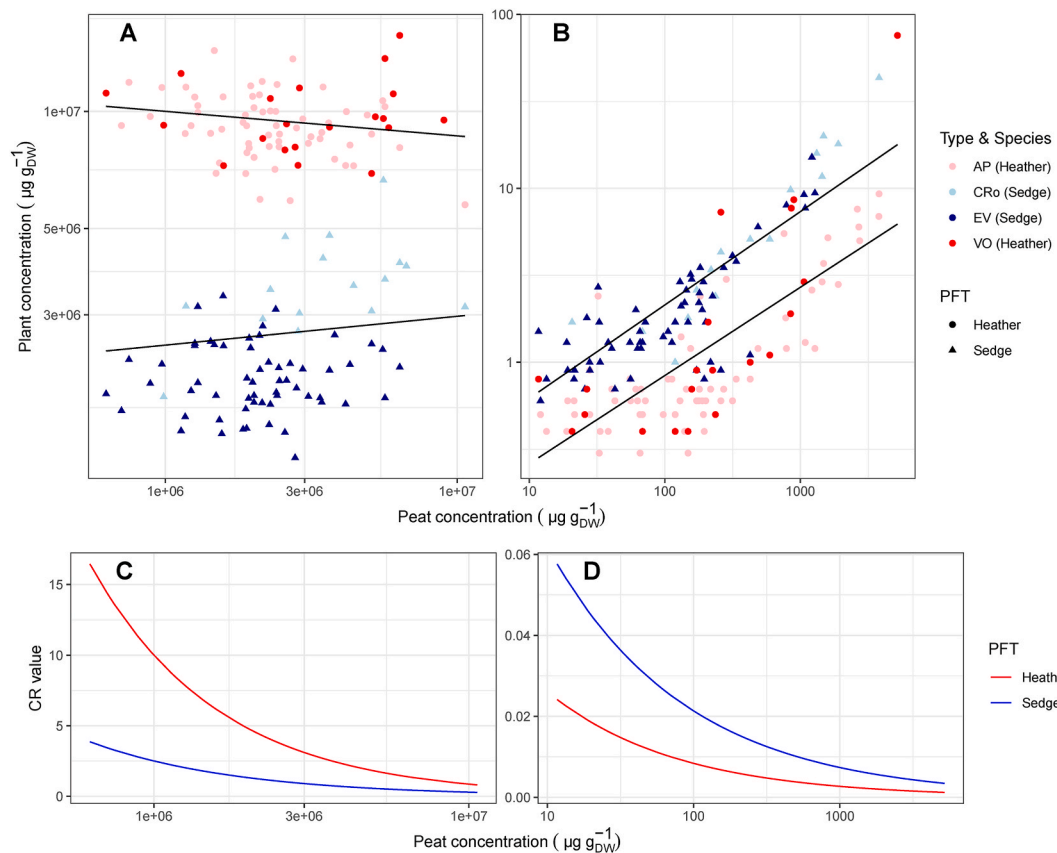


Fig. 4. Concentrations in the plants plotted against the concentrations in the peat for A) Ca and B) U as well as the ratio between concentrations of C) Ca and D) U in plants and peat (CR). Note the logarithmic scale in panels A and B.

3.3. EFFECTS OF ENVIRONMENTAL FACTORS ON CR

For two thirds of the examined elements, vegetation effects (i.e. PFT and species, 3 degrees of freedom) explained more variation in CR than the joint effect of the six examined environmental factors (elevation, peat depth, bulk density, C:N ratio, pH and electrical conductivity (EC)). Still, the CRs of all examined elements were affected by one or more environmental factors ($p < 0.05$). Most elements were affected by several factors and the direction of the effects tended to be shared among elements (Table 2). For example, the CR of 14 elements increased with the C/N ratio of peat, and the typical response to a 50 unit increase in C/N varied between a 50 % increase and a doubling of the CR value (25th and 75th percentiles). Similarly, for 11 of the 13 elements affected by peat depth, CR increased with depth, and the typical response varied between 20 and 40 % per 1 m depth increase. The CRs of nine elements were affected by pH, whereas EC and elevation affected seven elements, respectively. However, the responses to these three environmental variables (pH, EC and elevation) were mixed in both directions. Bulk density only affected the CR of three elements on top of the effects of the other environmental variables.

The effects of environmental factors on CR were either caused by a change in elemental concentration of the peat, a change in the elemental concentration in the plant, or a result of a combined response to concentrations in both soil and plants. Six elements, corresponding to radionuclides of particular interest for environmental impact assessments of repository safety, can be used to illustrate this point (Table S1). For all elements, the response of CR to C:N ratio, is primarily due to a decrease of elemental concentrations in peat, as plant concentrations in general appear to be insensitive to the N:C ratio ($|t\text{-value}| < 1$). In the case of U, where plant concentrations did decrease with an increasing N:C ratio, the response was much weaker than in the peat. It should also be noted that for Ca, which is a plant macronutrient, changes of all environmental factors had a marginal effect on plant concentrations ($|t\text{-values}| < 1.6$). Consequently, a decreasing CR with increasing pH, or with decreasing peat depth, was due to an increase in Ca concentrations in peat. For Mo, both plant and peat concentrations decreased with increasing peat depth, but the response in plants was much stronger than in peat; the overall effect was a decrease in CR with increasing peat depth. For Ni, Pb, Th and U, the responses of concentrations in plants and peat were similar in direction, but the response in peat was consistently stronger. Thus, with respect to the plant to peat concentrations ratios, the effect of environmental factors on the peat concentrations was somewhat dampened by concentrations in plants. Thorium is an exception to this pattern, as the response in CR to EC and bulk density appeared to be exclusively due to shifts in plant uptake.

3.4. THE RELATIONSHIP BETWEEN CONCENTRATIONS IN PLANTS AND PEAT

Although the elemental concentrations in plants were clearly correlated with the elemental concentrations in peat across all elements included in the study (Fig. 2b), the relationship varied strongly among different elements, and to some degree also between PFTs (Fig. 4). The strongest relationships were found among elements with low concentrations in plants and peat, and for these elements (e.g. U, Th, Pb, Cs, Ni and I) the power coefficient b tended to be around 0.5 (Table 3). This implies that a doubling of peat concentrations would result in a 40 % increase in the concentrations in plants. For several elements with high and medium concentrations in plants, the relationship was weaker, and occasionally not significantly different from zero (e.g. Ca, Mg, Zn and B; Table 3). There was also a tendency for a stronger plant-to-soil relationship among sedges as compared to heathers. The difference in response (b) between PFTs

Table 3

Effects of peat concentration on the plant concentration and CR for 19 elements. The strength of the plant-to-peat response is given by the exponent b , which is listed for heather and sedge PFTs. Bold numbers indicate that b is significantly different from zero ($p < 0.05$, t -test). For five elements b differs significantly between the two vegetation types (p -value given in separate column). The effect on CR to a reduction in peat concentration, by a factor of one standard deviation (on logarithmic scale), is expressed as the ratio between the CR given reduced and original peat concentrations.

Element	b ($C_{\text{plant}} \propto C_{\text{peat}}^b$)		p -value	Relative Response CR ($C_{\text{peat}}/\text{SD}$)		
	Heather	Sedge		Heather	Sedge	SD
B	0.14	0.12		1.3	1.4	1.4
Ba	0.17	0.61	>0.001	1.6	1.2	1.8
Ca	-0.06	0.07		1.9	1.7	1.8
Cs	0.39	0.52		1.3	1.3	1.6
Cu	0.06	0.28	>0.001	2.3	1.9	2.5
Fe	0.26	0.28		2.3	2.3	3.1
I	0.68	0.76		1.2	1.1	1.7
K	0.18	0.41	0.002	1.5	1.4	1.7
Mg	-0.09	-0.05		1.6	1.5	1.5
Mn	0.36	0.47		1.5	1.4	1.8
Mo	0.35	0.86	0.03	1.5	1.1	1.8
Ni	0.45	0.41		1.6	1.7	2.4
P	0.53	0.71		1.2	1.1	1.4
Pb	0.17	0.42	0.02	1.9	1.6	2.2
S	0.15	0.11		1.7	1.7	1.9
Sr	0.30	0.34		1.6	1.6	2.0
Th	0.61	0.78		1.4	1.2	2.6
U	0.51	0.54		2.2	2.1	4.8
Zn	0.06	0.21		1.5	1.4	1.6

was statistically significant for five elements (K, Ba, Cu, Mo and Pb, as indicated by a significant interaction between PFT and peat concentration), and for heather, the plant concentrations of two additional elements (Cu and Mo) were independent of the peat.

As the coefficient (b) for the plant-to-soil relationship was always below 1, the ratio between plant and peat concentrations decreased systematically with increasing peat concentration for all elements (shown for Ca and U in Fig. 4). To quantify the potential bias in CR caused by a shift in peat concentration, CR was calculated (Eq (3)). For each element, a moderate decrease in peat concentrations was used, corresponding to a division with the geometric standard deviation, to illustrate the expected shift in CR. The response in CR values ranged from an increase of 10 %–100 % (Table 3). The lower increase corresponds to elements showing a relatively strong plant-to-peat relationship and a relatively limited variation in peat concentrations (I and Mo in sedges). The higher response was either caused by a lack of plant-to-peat concentration relationship (Ca and Mg), or it was associated with elements showing a large environmental variation in peat concentrations (U). Thus, if a global CR was taken to represent a subset of mires with a relatively low peat concentration, the plant uptake in this environment would be underestimated by between 10 % and a factor of two, and the opposite would be true for environments with relatively high elemental concentrations in peat.

4. DISCUSSION

According to results of this study, the elemental concentrations in mire vegetation are typically correlated to the concentrations in peat. However, the plant functional type (PFT) and species, as well as environmental factors (especially pH), may have a strong effect on the variation in CR. For many elements, the PFT (heather and sedge) was more important for the differences in the CR than the plant species *per se*. The plants were sampled from shared locations, with similar availability of elements for the two PFTs. This implies that the observed differences may be explained by differences in the uptake and/or storage mechanisms between the PFTs, and for some elements, even between different species of the same type.

One explanation for the differences between PFTs could be that the heathers included in the study are mycorrhizal [45,46], while the sedges are not [45]. For many elements, mycorrhiza can regulate element uptake in plants [50–53]. Especially for macronutrients, the impact of mycorrhiza is typically positive [51–53]. While the results partly supported such mechanisms, the overall trend was not as straightforward, since the CR value for K was indeed higher in sedges, while P and S were equal, and Ca and Mg higher in heathers. However, some differences between the PFTs can also be explained by differences in plant morphology and physiological demands. For example, K is important for maintaining turgor pressure [54], which may be more important for leafy plants like sedges than woody heathers. In addition, differences in Ca between PFTs could be caused by higher Ca demand of woody stems found in heathers, compared to sedges which are lacking woody parts, as calcium availability affects wood formation [55]. Moreover, it is important to note, that cross-species comparison between mycorrhizal and non-mycorrhizal plant species may result in unexpected CR values also due to species-specific nutrient requirements, and the impact of mycorrhiza may vary depending on e.g. type of association and the nutrient status of the soil. For example, mycorrhiza may enhance Fe uptake when soil concentrations are low [56,57], but may not have any effect at higher Fe concentrations [57]. Thus, for essential elements, the differences in CR values may well be explained by factors related to specific plant nutrient requirements defined by plant species rather than mycorrhizal status. However, in regards of non-essential elements, three out of five elements (Pb, Th, U) that are toxic to plants, and not part of plant metabolism, were lower in the mycorrhizal heathers. This is well in line with the literature, as ericoid mycorrhiza has been suggested to decrease the uptake of elements that may be harmful to plants [50,58,59].

Another explanation for the differences in the plant concentrations could be rooting depth. The rooting depth of EV is around 50–60 cm [60,61], while for *Carex* sp. roots can extend down to 2 m depth [61]. For the heathers included in this study, the rooting depths are lower, with maximum rooting depth of 25–45 cm in AP [62,63], but only around 15 cm in *Vaccinium* sp [64]. Differences in rooting depth may favour sedges with access to elements from greater depth range, compared to heathers that rely on nutrient availability in the surficial peat. Since the elemental concentration depths-profiles were not available for the studied sites, the possibility for increasing plant nutrient availability with increasing peat depth cannot be excluded. Thus, based on the available literature, it can only be concluded that the variation in concentrations in plants is connected to factors related to plant physiology and morphology, as well as to external factors, such as, mycorrhizal interactions and variation in elemental concentrations along the peat depth profile.

Besides PFT, also plant species influenced the CR values. This observation is in accordance with several earlier studies showing similar variation in CR according to plant species [65–70]. Similar to the results here, Pillon et al. [67] found significant differences in elemental concentrations of plants among heather species growing at the same site for most of the elements included in their study [67]. However, while especially K was found in different concentrations across the species in the present study, K and Mo did not vary between the species included in Pillon et al. [67]. It should, however, be noted that Pillon et al. [67] and the present study cover different species, although representing the same PFT, which may explain these discrepancies for individual elements.

The results confirmed previous studies, which have shown non-linear plant uptake of elements compared to soil concentrations [31–34]. That is, the increases and decreases in elemental concentrations in plants were always weaker than those observed in elemental concentrations in the peat. A plausible explanation for non-essential elements is that the plant available fraction of an element is negatively correlated to the total soil concentration of that element. A negative relationship between soil sorption and plant uptake has been observed across multiple elements [68]. This relationship is expected because high soil sorption implies that an element is strongly retained by the soil and, thus, less available for plant uptake [2,71]. Such characteristics may be especially relevant in peat soils that have high cation exchange capacities. For essential elements, the lack of linearity is likely reflecting regulation of plant nutrient uptake relative to the plant nutrient demand. For example, levels of Ca and Mg need to be under strict control in order to maintain homeostasis inside plant cells [72]. The strongest environmental factor influencing the CR values was the C:N ratio of the

peat. For 14 out of 19 elements the CR increased with increasing C:N ratio, and in all of these cases this was due to lower elemental concentrations in peat with high C:N ratio. C:N ratios vary considerably among northern peatland types and ratios between 12 and 200 have been observed at individual sites [73]. The C:N ratio is typically high (>40:1) in vegetation and litter, but declines through the peat profile to reach ratios between 20:1 and 30:1 in peat below 50 cm [74]. The C:N ratio in peat decreases with the degree of humification, but the change is marginal once the process has progressed past the initial stages (von Post indices 3 to 7). Thus, it seems plausible that elemental concentration in peat increases as carbon is lost through aerobic and anaerobic decomposition and the bulk density of the material increases [25]. The C:N ratios have been reported to vary with approximately a factor of two among peatland categories globally [75], with the ratio decreasing from 33 in bogs to 28 in poor fens and 25 in rich fens in Canada [74]. In fact, it has been shown that in the beginning of the natural succession of a mire towards a more ombrotrophic state the elemental concentrations in the peat may increase [74,76], which would decrease the peat-to-plant transfer factor as stated above.

After the impact of C:N ratio on the CR was considered, the second most important factor influencing CR was peat depth, affecting the CR value of 13 elements. The impact of peat depth on the CR value was positive for all, except for two elements (Mo and S). This is logical as typically the elemental concentrations in peat become lower as the surface peat becomes more and more isolated from nutrient supply from the groundwater [77]. Further, for about half of the elements, the CR value decreased with increasing pH. Also this was likely due to a stronger response of peat than plants to a change in pH, as the sorption of cations is expected to increase with pH [78,79], making them less available for plants, and less likely to be flushed out of the peat [80]. Similar impact of pH has been reported by others on both sorption to soil *per se* [81], and on the plant availability [82].

The location at the mire (edge vs. center) had a weak impact on the CR, with higher CRs at the center of the mire for a handful of elements (Fe, Cs, Cu, Ba). The impact of the location at the mire was primarily related to the elemental concentrations in peat, which decreased towards the central parts of the mires with greater peat depth. This is consistent with a previous study at the mire chronosequence area [42]. A decrease in soil nutrient concentrations is expected towards the middle parts of the mires, where connection to the groundwater is weaker, and nutrient availability is more dependent on precipitation and internal nutrient transport within the mire area. Thus, in this study, environmental factors that lower the peat nutrient concentrations (decreasing pH, increasing C:N ratio, thicker peat depth, lower bulk density) consistently increased the CR value. This is in line with the discussion above that changes in the concentrations in plants were subtle compared to changes in the peat concentrations.

This study is presenting CR values for four mire plants representing two different PFTs, which is a significant addition to the literature reporting soil-to-plant element transfer in mire vegetation in natural (non-contaminated) conditions. The elements included in this study were divided into three groups; macronutrients, micronutrients and non-essential elements. The seven non-essential elements chosen for this study are all contaminants relevant for environmental impact assessment of a geological repository for radioactive waste. While the analyses here were made on the stable isotopes, we can assume that the results are readily applicable also for radionuclides [10,36]. While the concentrations in the plants for all elements broadly followed the concentrations in soil (though not all correlations were statistically significant), they had a slightly different behaviour regarding the connection between the concentration in plants and soil based on which group the element belonged to. Specifically, compared to the macronutrients, the micronutrients and especially non-essential elements correlated stronger with the concentration in soil. A regulated uptake of essential elements that are not growth limiting is expected to yield such non-linear response patterns between plant and soil concentrations. In this study, the concentrations in plants of several macro- (Ca, Mg) and micronutrients (B, Cu, Mo, Zn) were statistically unrelated to the concentrations in peat. This suggests that the availability of these elements exceeds plant needs, and that radionuclide uptake could indeed be estimated directly from the average elemental concentrations in the plants and the specific activity of the radionuclides in soil.

In earlier studies the correlations between concentrations of both micronutrients and non-essential elements in plants and soil have been variable. Some studies have found a correlation between the plant and soil concentrations for some of the elements studied here, including Cu, Mn, Ni, Pb and Zn [83,84], although in one of the studies the correlation was rather weak for Cu and Zn [85]. Yet another study reported no correlation for the concentration of Pb in plants and soil [71]. For macronutrients, the concentration of S in plants has been reported to correlate with soil concentration [86]. Raguz and co-workers [87] found that approximately a third of 61 examined elements showed strong evidence for a linear relationship between whole crop and soil concentrations in four agricultural fields in central Sweden. These elements included both micronutrients (e.g. Ni) and non-essential elements (e.g. Pb), but notably excluded macronutrients like Ca, K and Mg. The lack of elemental coverage, the limitation in sample sizes and the variability of the results in the few previous studies is highlighting the significant value of the present study in increasing the knowledge on the links between plant and soil concentrations over a range of elements and environmental conditions.

5. Conclusions

This study demonstrates a systematic variation in CR values of the included elements due to plant functional type, plant species and several environmental factors that primarily affect element concentrations in peat. Subsequently, it is reasonable to account for systematic differences in CR values between the PFTs addressed in this study, when the values are substantially different and the exposure pathways between the PFTs vary. The results also confirm that between-species variation in CR values may be substantial within a PFT, although this pattern may be different in other PFTs. Given the uncertainties regarding the structure and type of future vegetation communities, it is advisable to include between-species variation as a random component of the uncertainty tied to CR estimates. The fact that CR varies systematically with concentration in peat and several peat properties suggests that there is potential for a reduction of the uncertainties of empirically determined CR values. Moreover, in scenarios where the environment is postulated to change systematically in the future, functional relationships allow for an evidence based and sound adjustment of CR values. This is

particularly important to consider under circumstances when elemental concentrations in peat are expected to be significantly lower than average conditions. If CR values are assumed to be constant in such scenarios, there is a clear risk that assessment calculations will underestimate the transfer of contaminants from peat to plants.

CRedit authorship contribution statement

Sari Peura: Writing – original draft, Visualization, Investigation, Conceptualization. **Peter Saetre:** Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Betty Ehnvall:** Writing – review & editing, Visualization, Methodology, Data curation, Conceptualization. **Mats B. Nilsson:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Mats G. Öquist:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Conceptualization.

Data availability statement

Data will be made available upon request.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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