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Nutrient dynamics of drained peatland forests

CARL JOHAN WESTMAN[1] and RAIJA LAIHO[1,2,*]
[1]*Department of Forest Ecology, University of Helsinki, P.O. Box 27, FIN-00014 Helsinki, Finland;* [2]*Joensuu Research Centre, Finnish Forest Research Institute, Finland; *Author for correspondence (e-mail: raija.laiho@helsinki.fi; phone: +358-9-191-58139 or +358-40-587-5891; fax: +358-9-191-58100)*

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Abstract. Forest drainage has been used rather widely to improve tree growth in peatlands in northern and northeastern Europe and some parts of North America. The consequent fundamental change in the vegetation presumably gives rise to a concomitant change in the distribution of nutrients within the ecosystem. We investigated the post-drainage dynamics of soil properties (top 30-cm) and tree stand biomass on a series of peatlands drained for forestry in Finland to evaluate the sufficiency of soil nutrient pools for production forestry, and the ability of a floristic-ecological peatland site type classification for estimating soil nutrient status. The nutrient dynamics were assessed by comparing the nutrient pools in a large number of peatland sites differing in drainage age. Drainage unambiguously influenced stand biomass and structure and, consequently, the nutrient pool bound in trees. Nevertheless, with the exception of Mg, ditching did not decrease soil nutrient pools over the 75-year observation period. Thus, the soil pools seem sufficient for forest production on these sites. The decreasing trend in the soil Mg pool points on a potential risk in the long run, however. Peat depth and temperature sum were identified as significant sources of variation for the soil nutrient pools. Using soil Ca, K, Fe and N pools, on average 49% of our sites were grouped correctly according to the floristic-ecological site type classification. This classification most successfully described soil nutrient status among the most nutrient-poor sites. We concluded that the floristic-ecological classification of drained peatlands successfully describes their production potential, but not their total nutrient pools in varying thermoclimatic conditions.

Introduction

Peatlands are estimated to occupy roughly 500 million ha, or 3.8%, of the global land surface (Paavilainen and Päivänen 1995). Especially in the boreal zone, they form a considerable proportion of the forested landbase (Haavisto and Jeglum 1991; Paavilainen and Päivänen 1995; Dahl and Zoltai 1997). Some peatland types support commercially productive forests (Dahl and Zoltai 1997), but in general, tree growth is poor compared with upland forests. This is largely due to inadequate aeration of the rooting zone caused by persistently high water table levels.

Forest drainage has been used rather widely to improve tree growth in peatlands in northern and northeastern Europe and some parts of North America. The improved aeration of surface peat achieved with drainage (Silins and Rothwell 1999) strongly influences the ecosystem structure. The fundamental change in the vegetation (Laine et al. 1995a) presumably gives rise to a concomitant change in the distribution of nutrients within the ecosystem. In pristine peatlands, the peat-producing vegetation usually constitutes a relatively thin living layer where annual cycling of biomass and nutrients plays an important role (Bernard and Hankinson 1979; Urban and Eisenreich 1988; Verry and Urban 1992). After drainage, the growing tree stand becomes a considerable nutrient sink (Finér 1989), accumulating nutrients for a relatively long time – provided that the site is not too nutrient-poor to support tree growth (Vasander 1982). With harvesting, a nutrient pool that is considerable in some cases relative to the rooting zone soil pool is removed from the site (Kaunisto and Paavilainen 1988; Grigal and Brooks 1997).

So far, only a few, and none geographically extensive, investigations have been conducted on the influence of drainage on the nutrient balance of peatland forests (Kaunisto and Paavilainen 1988; Laiho and Laine (1994, 1995); Laiho et al. 1999).

The aim of this study was to evaluate 1) the sufficiency of soil nutrient pools for production forestry, and 2) the ability of a floristic-ecological peatland site type classification for estimating soil nutrient status in drained peatlands. To accomplish this, we investigated i) the post-drainage dynamics of surface peat soil properties and stand biomass, and ii) the distribution of nutrients between the peat and the developing tree stand on a series of peatlands drained for forestry in the southern part of Finland.

Material and methods

Sample sites

Selection of the sites to be sampled was based on the materials of several previous inventories as follows: i) a survey of peatlands drained for forestry by Keltikangas et al. (1986), ii) the 7th National Forest Inventory sample plot grid (e.g. Kuusela and Salminen (1991)), iii) a set of permanent sample plots in the research forests of the Finnish Forest Research Institute (see Gustavsen et al. (1998)) and iv) the SINKA network of permanent sample plots on drained peatlands (see Hökkä et al. (1997)). From these sources, we picked all sites meeting the following criteria: i) sites drained in 1978 or earlier, ii) depth of peat deposit of 0.3 m or more, iii) a tree stand having a basal area of 10 m^2 ha^{-1} or more of pine or spruce and iv) no cuttings during a previous ten-year period. Altogether 572 sites scattered over the southern part of Finland were inventoried (Figure 1).

On every approved site (statistical unit), one relascope sample plot was measured. The size of the relascope plot depends on the DBH distribution of the tree stand: big trees are counted from a larger area than small trees. In our material, the smallest plot was 50.2 m^2 (4 m radius) and the largest 1661.1 m^2 (23 m radius). The plot was located so that the distance between the midpoint of the plot and the nearest ditch was 1/3 of the spacing between adjacent ditches. In case the site was

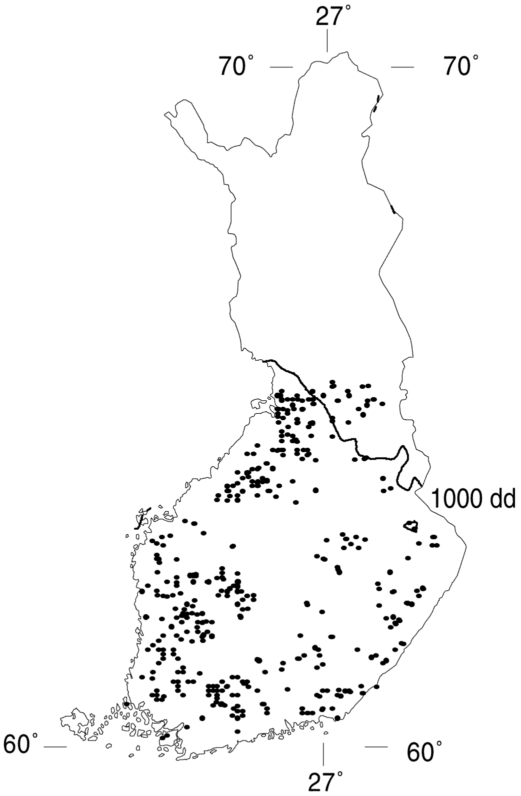

Figure 1. Distribution of our sample sites. A borderline of 1000 dd accumulative temperature sum (5 °C threshold value) is indicated.

drained with only one ditch, the distance to the peatland/upland margin was used for locating the sample plot.

For each sample plot, the following descriptive properties were determined: i) geographical location and height above sea level, ii) depth of peat layer (down to 1.5 m), iii) time of drainage and iv) drained peatland forest site type: Herb-rich type (**HrT**), *Vaccinium myrtillus* types 1 and 2 (**MT1, MT2**), *Vaccinium vitis-idaea* types 1 and 2 (**VT1, VT2**) and Dwarf-shrub type (**DsT**) (according to Laine (1989)).

Forests classified as HrT develop from the most fertile spruce mire sites after ditching. Tall ferns (e.g. *Athyrium filix-femina*) and herb species (e.g. *Oxalis acetosella*) characterize the ground vegetation. MT types are characterized by the dominance of *Vaccinium myrtillus* and *V. vitis-idaea* in the field layer. Herbs typical of mesic upland sites (e.g. *Trientalis europaea*) are also indicative species. MT1 develops from forested spruce mire sites and has typically *Lignum-Sphagnum* peat, whereas MT2 develops from mesotrophic treeless sites or composite pine mire sites, having the properties of both treeless and forested sites, typically with *Carex*-peat. VT types have dwarf-shrubs typical of pine mires (*Ledum palustre* and *Vaccinium* *uliginosum* on VT1, mainly *Betula nana* on VT2) growing scattered amongst the *V. vitis-idaea* and *V. myrtillus*-dominated field layer community. VT1 develops from the least fertile spruce mires and minerotrophic pine mires, having *Sphagnum* residue-dominated peat. VT2 develops from treeless sites or composite oligotrophic tall-sedge mires and has peat made up mainly of *Carex* residues. Forests classified as DsT develop from ombrotrophic pine mire sites. Pine mire dwarf-shrubs are dominant in the field layer. Peat consists of *Sphagnum* and *Eriophorum vaginatum* remains.

These site types form a post-drainage production potential gradient, HrT being the most productive and DsT the least productive type (Laine 1989). Norway spruce (*Picea abies*) dominance or co-dominance with birch (*Betula pubescens*) on the most fertile sites (HrT, MT1) gradually changes to Scots pine (*Pinus sylvestris*) dominance on poor sites (DsT). No clear differences in potential productivity have been assumed between the types 1 and 2 of MT and VT. These types have been divided largely because of, due to their more genuine mire origin, nutrient imbalances and other silvicultural problems related to tree stand composition being more common in type 2 (Laine 1989). Consequently, the potential productivity of some type 2 sites will not be realized at least during the first, pre-drainage origin, tree stand generation after drainage.

Sampling and measurements

On each sample plot, the basal area of the tree stand was measured by tree species, and the breast height diameter of each tallied tree was measured. From ten sample trees, tree age, height, diameter at 6 m, and thickness of bark were also measured. The thickness of the peat deposit was recorded to a depth of 1.5 m.

Ten volumetric soil cores (1500 cm^3 each) per plot were taken to a depth of 30 cm from randomly chosen locations. The cores were extracted with a slightly conical cylinder having a saw-toothed cutting edge. The samples were then combined across plots to form composite samples. Prior to sampling, the green part of mosses and other living surface vegetation was removed. However, fine roots were not extracted from the sample. On sites with shallow peat, when the corer occasionally reached underlying mineral soil, the length of the sampled peat monolith was recorded.

The sampled 0–30 cm layer is functionally the rooting zone of trees in both undrained and drained peatland sites (Holmen 1964; Paavilainen 1966; Paavilainen and Päivänen 1995; Lieffers and Rothwell 1987; Laiho and Finér 1996). The maximum rooting depth may be slightly deeper in well-drained spruce- or birch-dominated sites, and less in the most nutrient-poor and acid pine sites (Holmen 1964; Heikurainen 1955; Paavilainen 1966).

In the laboratory, the samples were dried to constant mass at 105 °C, weighed and then homogenized in a hammer mill supplied with a 2-mm sieve. A sub-sample from the homogenized sample was used for further analyses. Loss on ignition was determined by igniting a sample to constant mass at 550 °C. Acidity was measured as pH in a suspension of 10 ml soil and 25 ml 0.01 M $CaCl_2$ after over night standstill. Cation exchange capacity (CEC) was determined by extracting 4 g of soil with 200 ml non-buffered 1 M KCl. From the filtrate, calcium (Ca) and magnesium (Mg) were determined by NaEDTA complexometric titration, and aluminum (Al) and hydrogen (H) by consecutive titration with NaOH and HCl. Effective cation exchange capacity was calculated as the sum of acidic and basic ions. Base saturation (BS) was evaluated as the percentage of Ca-Mg out of total exchange. The total content of nitrogen (N) in peat was determined by steam distillation after Kjeldahl digestion (370 °C) of a sub-sample in H_2SO_4 with Na_2SO_4 as catalyst. The total contents of phosphorus (P), potassium (K), Ca, Mg, manganese (Mn) and iron (Fe) were determined by digesting (212 °C) a sub-sample in H_2SO_4-HNO_3-$HClO_4$ acid solution. From the digest, P was determined colorimetrically by the molybdenum-blue method, K by flame photometry and other elements by atomic adsorption spectrophotometry.

Calculations and preliminary treatment of material

On the basis of the sample tree data and the breast height diameter distribution of the tally trees, stand basal area, mean height, and volume were calculated with the KPL programme of the Finnish Forest Research Institute.

For each breast height diameter class, the biomass was estimated by applying allometric regression functions using breast height diameter as the explanatory variable. The biomass of roots, stump, trunk, branches, bark and needles were estimated using Marklund (1988) functions, that have been concluded to produce feasible estimates for peatland stands by Minkkinen et al. (2001). For roots and stump we used a procedure described by Minkkinen et al. (2001) to adjust for the higher biomass allocation to below-ground parts by trees growing on peatlands (Laiho and Finér 1996). By multiplying with the respective nutrient concentration, the nutrient content of each component was then estimated. Nutrient concentrations were taken from Finér (1989, 1991) data on MT1, MT2, VT2 and DsT sites. The data on MT1 were used for HrT, and that of VT2 for VT1, as these were the closest equivalents available. Finally, the total tree stand biomass and nutrient pool (g m^{-2}) were obtained by multiplying the average tree estimates with the number of trees in the respective diameter class, and summing the diameter class values.

An estimate for the local temperature climate was obtained by calculating the accumulative temperature sum (5 °C threshold value) for each site using a trend surface equation (Ojansuu and Henttonen 1983) and the geographical location and elevation as explanatory variables.

Drainage age (time period between ditching and field measurement) was transformed into a class variable with 10-year intervals. Although some site-level information was lost by this operation, considerable noise in the data was eliminated.

An obvious relation existed between peat depth and ash content of the peat in the material. Generally, high ash values were concentrated in sites where the peat depth was less than 0.6 m, and the deeper the peat deposit, the lower the ash content. However, high ash values were also occasionally found on sites with a deep peat layer. In such cases, minerogenic soil material may have been deposited upon

Table 1. Main study material. Number of sampled sites by drained peatland forest type and years since drainage after exclusion of sites with high ash concentration.

Drained peatland forest type[1]	Years since drainage							
	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80
HrT	2	18	11	5	8	3	4	2
MT1	5	24	18	9	22	4	1	2
MT2	2	22	15	2	6	6	2	3
VT1	2	42	17	2	9	1	–	–
VT2	2	45	24	8	23	8	1	3
DsT	10	56	17	7	27	5	3	2

[1] HrT = Herb-rich type, MT1 and MT2 = *Vaccinium myrtillus* types 1 and 2, VT1 and VT2 = *V. vitis-idaea* types 1 and 2, DsT = Dwarf-shrub type.

flooding or been spread as an ameliorative if the site was originally intended for agricultural use. Even ancient wild fires may have resulted in peat layers with high ash content. Since we were attempting to evaluate the general prerequisites for forest production on genuine peat soil, we decided to treat those sites with peat showing unexpectedly high ash concentration as a separate population in our statistical testing. To do so, we applied the SYSTAT stem and leaf procedure to distinguish outliers. As ash concentration distribution is dependent on site type (Westman 1981), outliers were detected separately for each drained peatland forest type. With the exception of the poorest site type, the detected outliers were mostly scattered high values. For DsT, the ash frequency distribution was not only strongly skewed but also highly peaked. Consequently, in this group relatively many observations were excluded.

After eliminating sites with outside ash concentration in soil, a total of 510 sites remained (Table 1). Two thirds of the sites (70.3 %) were dominated by Scots pine. Less than one fourth (23.6 %) were Norway spruce stands and the remainder were dominated by birch, mostly pubescent birch. Tree stand volume on the sites varied from a minimum of 13.9 $m^3\ ha^{-1}$ to a maximum of 361 $m^3\ ha^{-1}$, and the average by type volume increased consistently from DsT to HrT along the production potential gradient.

Statistical analyses

First, differences in soil and tree stand properties within the site type and drainage age gradients were tested using analysis of variance, where peatland forest type and drainage age were used as grouping factors. The distributions of both soil and tree stand nutrient pools were clearly non-normal, and their variances differed among site types. A logarithmic transformation brought the distributions closer to normality but could not totally remedy the heteroscedasticity. Consequently, Dunnett's T3 test, which does not assume equal variances, was used for pairwise comparisons of means.

Second, the effects of temperature sum and depth of the peat deposit on soil nutrient pools and stand properties were tested using analysis of covariance. As site type turned out to be a highly significant main effect on most soil and stand variables, and the effect slopes of temperature sum and depth of the peat deposit were not homogenous among site types, these tests were done by site type. Drainage age was used as a categorical variable to ensure that a significant age effect would not be masked by variation in temperature sums or peat depth.

Discriminant analysis was used to investigate whether, and if so, how soil nutrient regimes differ among the floristic-ecological site types. A jackknifed classification matrix was used to cross-validate the estimates of how the sites would be classified according to their soil nutrient pools, and which proportion would be classified "correctly", as compared with the floristic-ecological classification. Both a complete estimation with all measured elements and a step-wise analysis with probability limit 0.001 to-enter and 0.05 to-remove were performed. A restrictive to-enter probability was used because some of the nutrient pools are strongly interrelated.

SYSTAT 8.0 and SPSS 8.0 for Windows were used to perform the analyses.

Results

Stand biomass estimates

The estimated aboveground stand biomass of our sites varied from 1.1 kg m^{-2} to 19.8 kg m^{-2}, and the estimated root biomass between 0.3 and 7.6 kg m^{-2}. Stand biomass clearly reflected the productivity gradient. Thus, the average aboveground stand biomass increased from 4.7 kg m^{-2} in DsT to 11.0 kg m^{-2} in HrT (Figure 2). The corresponding root biomass increased from 1.6 to 3.7 kg m^{-2}.

Within all site types, except DsT, biomass of tree stands decreased significantly with decreasing temperature sum. A trend of tree biomass increasing with decreasing peat depth also was present; this trend was most evident on MT2 and DsT sites.

Drainage age had a highly significant main effect on tree stand biomass; among MT2, VT2 and DsT, in particular, biomass tended to increase along with increasing drainage age (Figure 2). Although the average initial biomass varied only slightly between MT2, VT2 and DsT site types, the rate of post-drainage biomass accumulation was different between these three site types (Table 2). Thus, over the 75-year period covered by our sampling, an average of 7.5 kg m^{-2} aboveground tree biomass accumulated on the MT2 sites. The corresponding amount for VT2 sites was 4.9 kg m^{-2}, and for DsT sites only 2.2 kg m^{-2}.

The increase in biomass was mainly allocated to stem wood. The mass of the needle fraction on pine-dominated VT2 and DsT sites remained unaffected on a 0.3 to 0.5 kg m^{-2} level. For MT2, the initial mass of needles was approximately the same as for VT2 and DsT sites, but over time tended to reach a level common for HrT and MT1 (some 1.0 kg m^{-2}). This increase in needle biomass on MT2 sites

Table 2. Regression between tree stand biomass (kg m^{-2}) and drainage age. The regressions are calculated with drainage age class as an independent variable and average age class biomass as a dependent variable.

Drained peatland forest type	Constant	Coeff.	$t_{\text{coeff.}}$	$F_{\text{regr.}}$	R^2
MT2	3.83	0.106	3.95^{**}	25.34^{**}	0.81
VT2	4.09	0.065	5.31^{**}	15.98^{**}	0.72
DsT	4.21	0.029	10.32^{***}	10.74^{*}	0.64

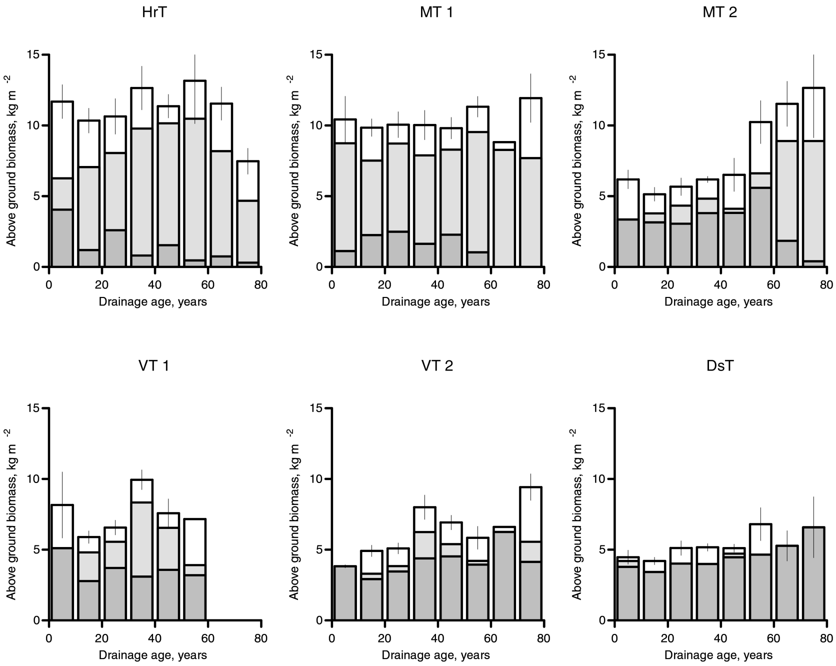
HrT
MT 1
MT 2
VT 1
VT 2
DsT

Figure 2. Mean aboveground stand biomass and s.e.m. by drainage age for the six drained peatland forest types. The dark grey area indicates the biomass of Scots pine, the light grey area that of Norway spruce and the open area that of broad-leaved trees (mostly pubescent birch).

was a result of stand development towards spruce dominance (Figure 2). The most obvious changes in tree species composition were found for HrT and MT2; birch was a receding species on HrT sites, and pine correspondingly on MT2 sites.

An increase in root biomass also occurred with increasing drainage age. The increase was most pronounced on MT2, VT2 and DsT; we estimated a doubling of the root biomass fraction over the investigated 75-year period. In the two most fertile site types, having well-developed tree stands already at the time of drainage, the estimated root biomass did not change upon drainage.

Nutrient pools

Productivity gradient

We found an abundant N pool in the top 30 cm of the soil ranging between 103 and 1815 g m^{-2} (Figure 3), whereas P (5.5–205 g m^{-2}) and K (4.9–290 g m^{-2}) pools were rather scant (Figures 4 and 5). The pools of Ca and Mg were more variable, ranging from 13 to 1240 g m^{-2} for Ca and from 2.6 to 546 g m^{-2} for Mg (Figures 6 and 7). However, the element showing the most extreme variation was Fe (Table 3). The Mn pool was on average low, although in some scattered cases, very high values were found (Table 3).

For all elements, the soil pools varied significantly among peatland site types (Table A1). Generally, soil nutrient pools decreased along the productivity gradient from HrT to DsT (Figures 3, 4, 5, 6 and 7). The relations between MT and VT types 1 and 2 varied, however. Although types 1 and 2 did not differ from each other with respect to soil P, Ca, Mg and Mn pools, the peat N pool on sites originating from composite types, MT2 and VT2, seemed to be somewhat higher than on sites of the genuinely forested peatlands, MT1 and VT1 ($p = 0.072$ for MTs, $p = 0.024$ for VTs). The same phenomenon was even clearer in the Fe pools ($p < 0.001$ for both MTs and VTs). In contrast, MT1 and VT1 had clearly higher K pools than MT2 and VT2 ($p = 0.002$ for MTs and $p = 0.001$ for VTs).

Although an analysis of variance indicated significant between site type variation (Table A1), CEC differed little between individual types and no clear site fertility-related trend was seen (Table 4). In contrast, BS increased with increasing site fertility (Tables A1 and 4). Correspondingly, soil pH indicated a trend of decreasing acidity with increasing site fertility (Tables A1 and 4). Thus, in cases when relatively more base cations were attached to the exchange sites, also pH was high ($r = 0.687$). With respect to both pH and BS, MT1 related more closely to the less productive *Vaccinium* types than to MT2.

In general, the pools of N, P and K, and BS in the top 30 cm of soil decreased with increasing thickness of peat deposit (Table A2).

Of all soil element pools studied, our sites were best separated by Ca and K pools (F-to-enter 65.2 and 26.2, respectively), followed by Fe (F-to-enter 21.6) and N (F-to-enter 9.2) (Figure 8). Using these four pools, on average 49% of the sites were grouped correctly according to the surface vegetation-based site type classification (Table 5). The MT1 site type reflected the soil properties the least: 26% of all possible cases were allocated to their respective site type on the basis of nutrient pools. The best fit between vegetation composition and soil nutrient regime was found among DsT sites. In this case, soil pools of Ca, K, Fe and N allocated 70% to their respective site type. The first canonical variable (eigenvalue 1.011) accounted for 71% of the total dispersion of the site types, and the second variable (eigenvalue 0.300) for 24%. Using all studied elements in the analysis did not affect the proportions of sites classified correctly.

Because of more productive sites, and dominance of Norway spruce, the tree stands on HrT and MT1 were distinguishable from stands on VT1, VT2 and DsT by having more nutrients accumulated in the stand (Figures 3, 4, 5, 6 and 7).

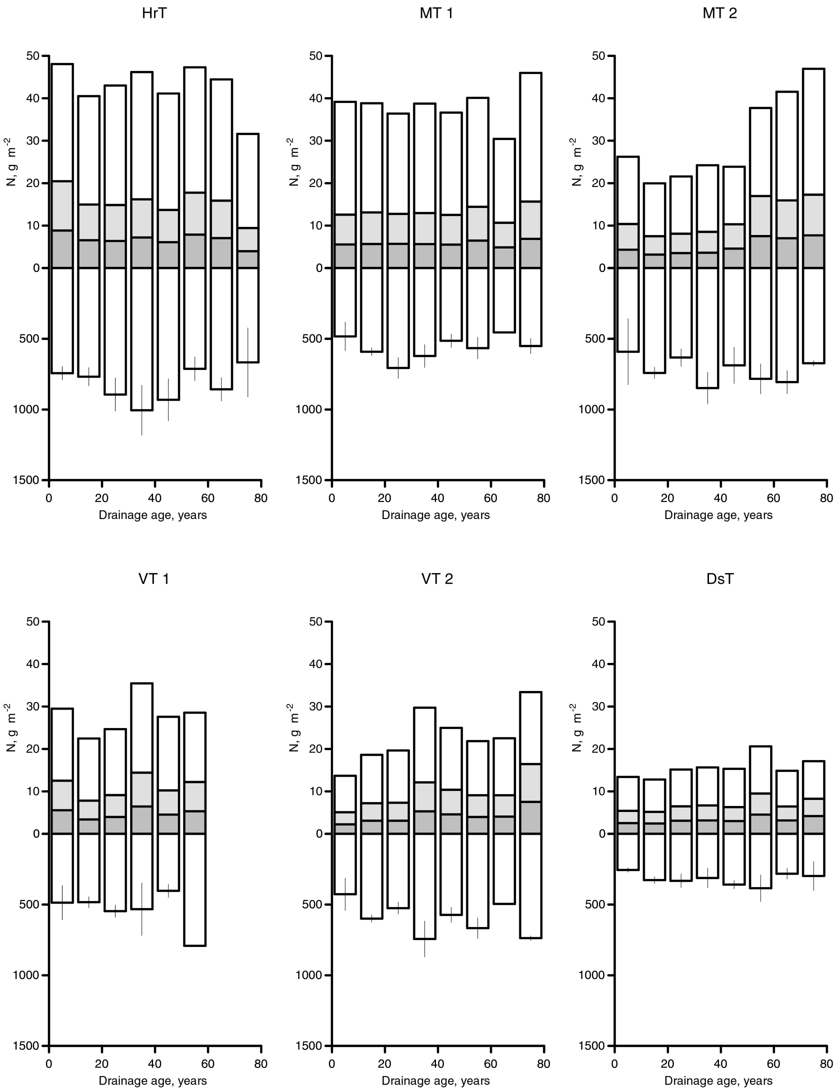

Figure 3. Mean nitrogen pools (g m^{-2}) in different compartments of drained peatland forests in relation to drainage age for six drained peatland forest types. Bars with whiskers below zero level represent mean pool in the top 30-cm soil layer and s.e.m. Stacked bars above zero level are estimated pools in tree roots (dark grey), stem and branches (light grey) and needles (no shading). Note change in Y-axis scale at zero level.

North – South gradient

The large geographical spread of our sites (Figure 1) gave rise to a wide range in local temperature climate. Consequently, the accumulative temperature sum varied from 817 dd in the north to 1360 dd in the south. The temperature sum was a significant covariate for soil N, P, Fe and Mn pools, and pH (Table A2). All of these

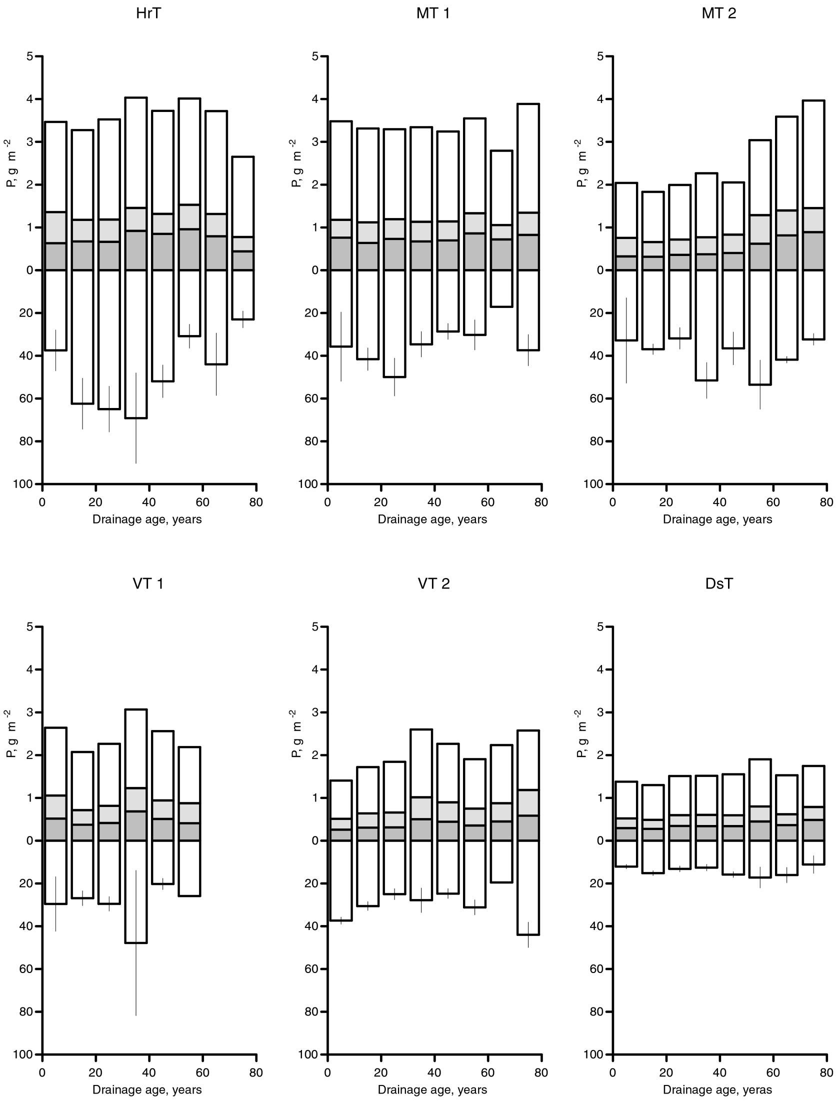

Figure 4. Mean phosphorus pools (g m^{-2}) in different compartments of drained peatland forests in relation to drainage age for six drained peatland forest types. See Figure 3 for explanations.

pools as well as soil pH increased with decreasing temperature sum. For N, the effect was most pronounced for the less productive types (not significant for HrT and MT1 types). The opposite was true for Mn.

Tree stand nutrient pools followed the trends in stand biomass: they decreased linearly with decreasing temperature sum. DsT was an exception for which no effect of temperature sum was observed.

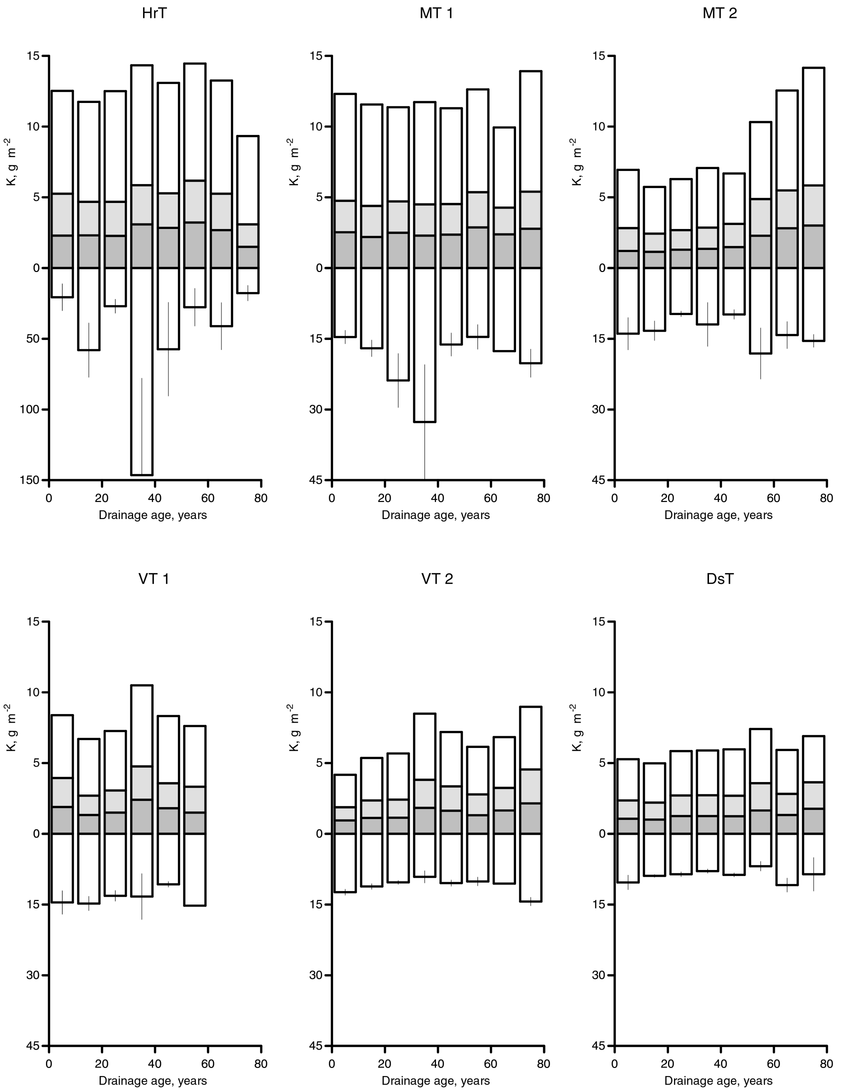

Figure 5. Mean potassium pools (g m^{-2}) in different compartments of drained peatland forests in relation to drainage age for six drained peatland forest types. See Figure 3 for explanations. Note the different scale of Y-axis for soil K for Herb-rich type.

Drainage age gradient

Within each site type, element pools both in soil and tree stand varied substantially among drainage age classes (Figures 3, 4, 5, 6 and 7). However, for the elements in soil, only variation in Mg and Fe pools was significantly explained by drainage age (Table A1). After an initial rise (up to 35 years), soil Mg pool decreased on average with increasing drainage age. Soil Fe pool varied rather inconsistently among drain-

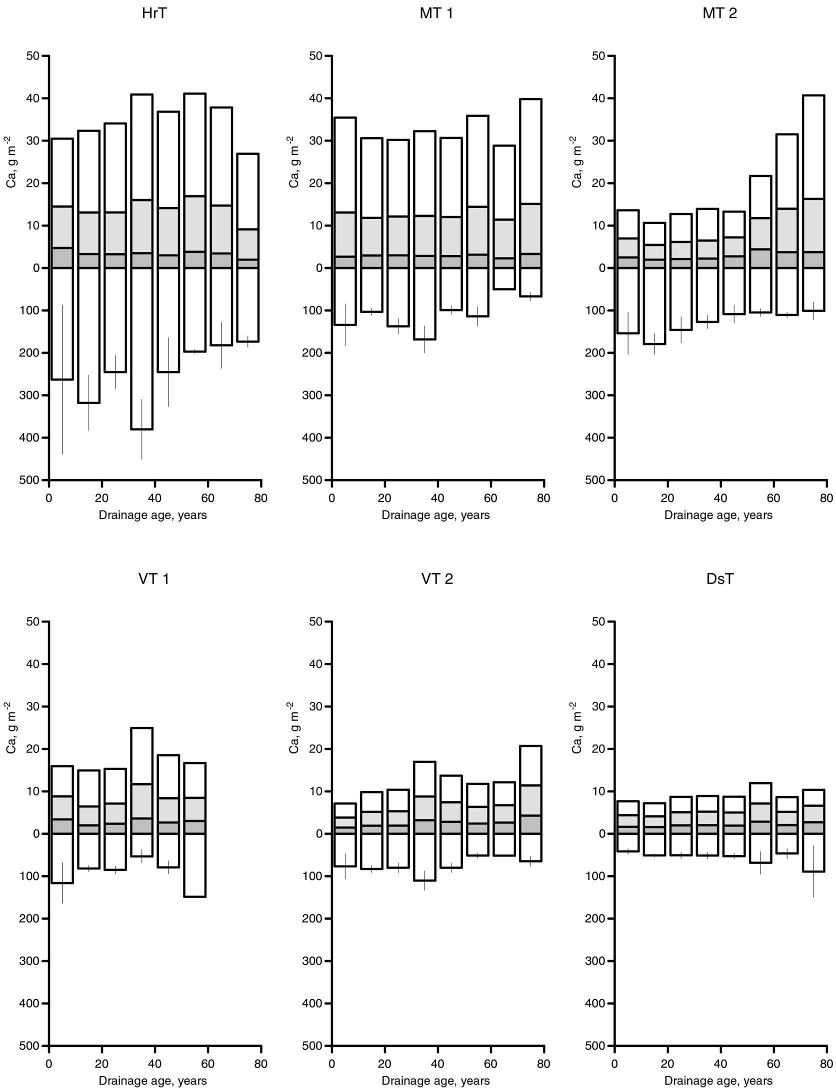

Figure 6. Mean calcium pools (g m^{-2}) in different compartments of drained peatland forests in relation to drainage age for six drained peatland forest types. See Figure 3 for explanations.

age age classes. For Mn, a significant interaction was revealed between site type and drainage age; however, when tested separately for each site type, no significant age effects could be found.

Soil pH decreased significantly after drainage (Table A1). This was especially pronounced on the initially least acid sites; for DsT, a non-significant increasing trend was observed. Similar, but non-significant, trends were found for BS.

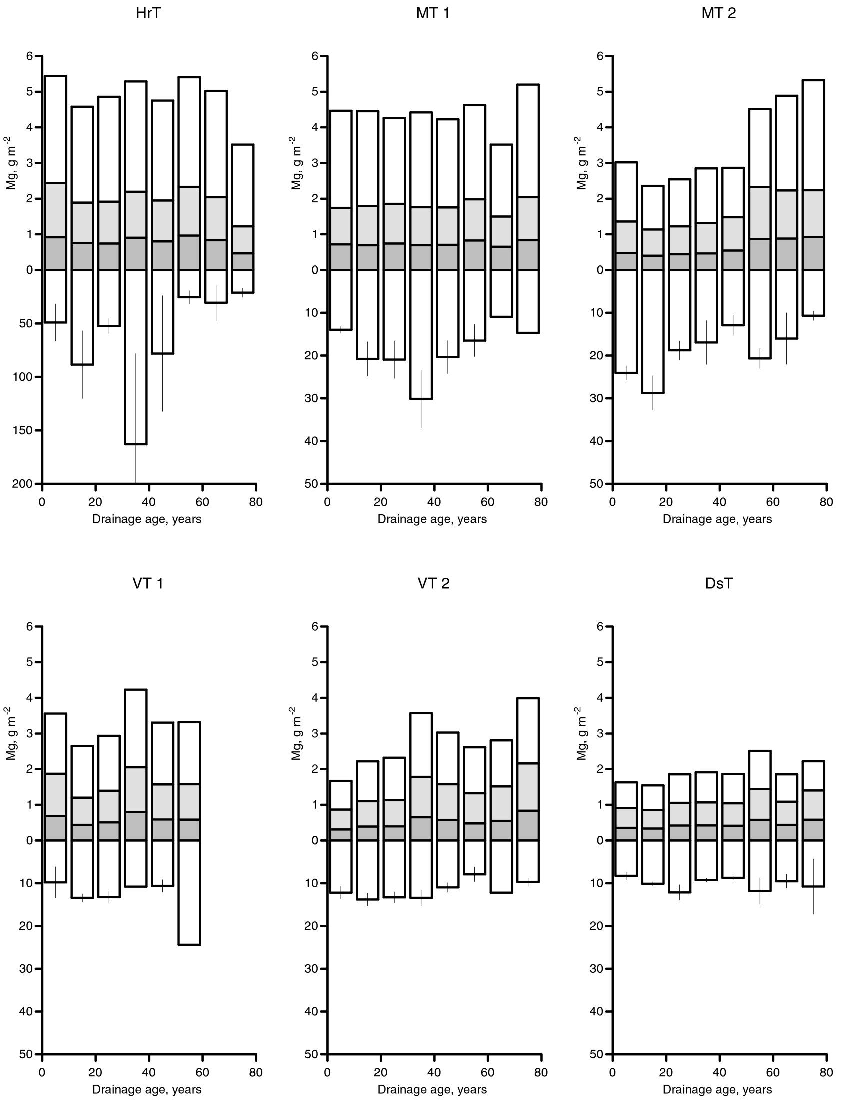

Figure 7. Mean magnesium pools (g m^{-2}) in different compartments of drained peatland forests in relation to drainage age for six drained peatland forest types. See Figure 3 for explanations. Note the different scale of Y-axis for soil Mg for Herb-rich type.

For elements bound in the tree stand, drainage age contributed significantly (K, Ca) or almost significantly (N, P, and Mg), to variance models. Especially on MT2 sites, the amount of nutrients bound in the tree stand increased significantly with increasing drainage age. Thus, on recently drained sites, the amount was of the same magnitude as on less productive sites, and on sites drained 40 to 80 years ago, the bound amount equaled that of the most productive sites.

Table 3. Pools of manganese (Mn, g m^{-2}) and iron (Fe, kg m^{-2}) in the topmost 30-cm peat layer. Means and standard errors of means by drained peatland forest type and drainage age class. Underlined cell values indicate singular observations which strongly deviate from the bulk of observations.

Drained peatland forest type	Years since drainage							
	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80
	Mn							
HrT	77.4 ± 76.8	14.83 ± 9.24	10.76 ± 2.78	47.5 ± 37.8	4.93 ± 2.26	5.61 ± 2.91	5.15 ± 2.90	3.46 ± 2.55
MT1	1.71 ± 0.33	2.08 ± 0.33	2.46 ± 0.52	2.35 ± 0.72	1.91 ± 0.33	3.43 ± 1.58	1.19	2.97 ± 1.11
MT2	1.27 ± 0.65	7.52 ± 3.60	2.02 ± 0.56	3.11 ± 0.22	1.51 ± 0.52	2.47 ± .44	1.14 ± 0.51	3.29 ± 1.23
VT1	0.82 ± 0.37	1.56 ± 0.25	1.12 ± 0.14	0.96 ± 0.34	1.33 ± 0.18	2.59	–	–
VT2	1.75 ± 0.97	1.20 ± 0.13	1.98 ± 0.46	2.35 ± 0.84	1.28 ± 0.14	0.74 ± 0.07	2.11	1.77 ± 0.91
DsT	0.96 ± 0.27	0.90 ± 0.07	1.00 ± 0.08	0.89 ± 0.16	0.86 ± 0.09	0.64 ± 0.13	0.89 ± 0.19	1.44 ± 1.10
	Fe							
HrT	485 ± 352	612 ± 170	715 ± 217	679 ± 255	432 ± 217	144 ± 31	204 ± 115	172 ± 98
MT1	65 ± 23	172 ± 47	242 ± 68	311 ± 150	111 ± 32	553 ± 363	55	92 ± 12
MT2	96 ± 23	502 ± 100	196 ± 41	443 ± 114	201 ± 48	641 ± 269	203 ± 145	197 ± 86
VT1	20 ± 0	75 ± 15	133 ± 51	32 ± 16	41 ± 6	1040	–	–
VT2	43 ± 1	132 ± 19	161 ± 36	210 ± 47	124 ± 22	272 ± 99	57	212 ± 126
DsT	22 ± 3	49 ± 7	395	31 ± 7	44 ± 6	35 ± 15	27 ± 3	21 ± 15

Table 4. Soil cation exchange capacity (CEC, mmol(+) kg^{-1}), base saturation (BS, %) and acidity (pH in 0.01 M $CaCl_2$). Means and standard errors of means by drained peatland forest type and drainage age class. Underlined cell values indicate singular observations which strongly deviate from the bulk of observations.

Drained peatland forest type	Years since drainage							
	1–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80
	CEC							
HrT	359 ± 76	346 ± 18	356 ± 24	372 ± 61	340 ± 20	353 ± 24	356 ± 16	350 ± 83
MT1	371 ± 25	323 ± 11	349 ± 15	364 ± 13	320 ± 12	337 ± 7	374	275 ± 42
MT2	337 ± 82	337 ± 19	315 ± 24	295 ± 22	319 ± 46	310 ± 22	316 ± 35	284 ± 26
VT1	290 ± 19	305 ± 8	295 ± 10	315 ± 4	305 ± 18	476	–	–
VT2	358 ± 41	289 ± 8	303 ± 11	317 ± 24	297 ± 9	268 ± 17	266	234 ± 17
DsT	322 ± 18	304 ± 8	313 ± 11	333 ± 41	293 ± 9	323 ± 32	333 ± 37	356 ± 59
	BS							
HrT	63 ± 20.8	51 ± 5.5	52 ± 5.6	52 ± 15.7	42 ± 7.4	49 ± 6.7	37 ± 9.1	54 ± 15.1
MT1	42 ± 7.7	33 ± 1.7	33 ± 3.4	41 ± 3.4	36 ± 2.5	38 ± 5.4	21	29 ± 2.3
MT2	54 ± 18.7	48 ± 4.0	45 ± 5.0	38 ± 9.3	38 ± 7.1	33 ± 1.7	29 ± 1.7	28 ± 5.9
VT1	44 ± 14.0	32 ± 1.7	32 ± 2.6	26 ± 10.9	35 ± 3.8	45	–	–
VT2	26 ± 11.3	32 ± 2.1	34 ± 2.8	32 ± 4.1	33 ± 2.4	24 ± 2.0	26	22 ± 3.2
DsT	24 ± 2.3	28 ± 1.0	27 ± 2.4	25 ± 3.0	29 ± 2.0	27 ± 5.6	32 ± 4.2	39 ± 11.8
	pH[1]							
HrT	3.6 ± 0.18	3.5 ± 0.09	3.8 ± 0.11	3.4 ± 0.33	3.3 ± 0.11	3.3 ± 0.08	3.0 ± 0.20	3.5 ± 0.05
MT1	3.3 ± 0.11	3.2 ± 0.05	3.2 ± 0.07	3.3 ± 0.07	3.1 ± 0.05	3.2 ± 0.13	2.7	3.1 ± 0.05
MT2	3.6 ± 0.18	3.5 ± 0.08	3.3 ± 0.14	3.5 ± 0.00	3.4 ± 0.11	3.2 ± 0.20	3.2 ± 0.11	3.1 ± 0.15
VT1	3.3 ± 0.18	3.0 ± 0.03	3.2 ± 0.04	3.1 ± 0.11	3.1 ± 0.05	3.6	–	–
VT2	3.1 ± 0.24	3.1 ± 0.04	3.1 ± 0.06	3.1 ± 0.11	3.1 ± 0.05	3.2 ± 0.06	2.7	3.1 ± 0.10
DsT	2.8 ± 0.05	2.8 ± 0.03	2.8 ± 0.05	2.8 ± 0.08	2.9 ± 0.04	2.8 ± 0.09	2.9 ± 0.04	3.0 ± 0.11

[1] Calculated from hydrogen ion concentrations.

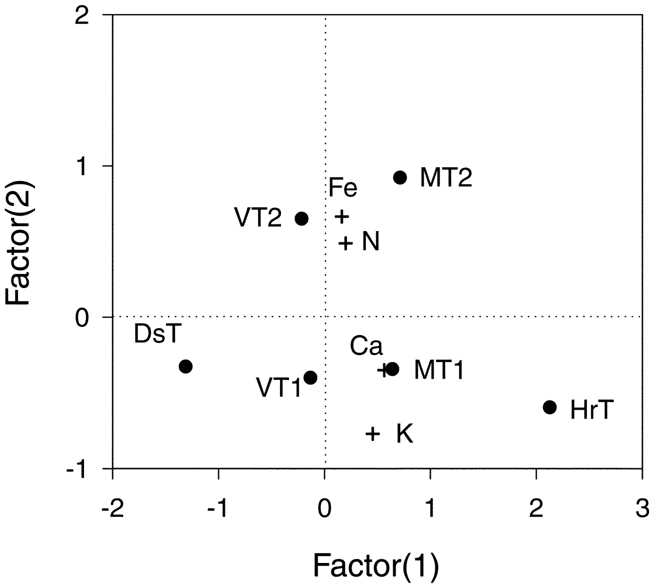

Figure 8. Standardized canonical discriminant function coefficients for classifying variables (nutrients), and functions at group (site type) centroids.

Table 5. Classification matrix showing the allocation of sites to the predefined site types by soil nutrient pools using stepwise discriminant analysis.

Actual site type	Predicted site type, %						% correct
	HrT	MT1	MT2	VT1	VT2	DsT	
HrT	54	21	17	0	4	4	54
MT1	15	26	14	31	8	6	26
MT2	9	14	55	3	10	9	55
VT1	3	18	5	38	15	21	38
VT2	2	8	22	11	44	13	44
DsT	0	1	4	14	11	70	70
All	*10*	*13*	*17*	*17*	*18*	*26*	*49*

Nutrient distribution

Nitrogen and P pools in soil were large in comparison with the amounts bound in aboveground tree biomass (Figures 3 and 4). Depending on site type, the amount of N bound in biomass made up only some 2–7% of the total amount in soil. For P, the respective range was 3–12% (Figure 9). For Ca and Mg, the corresponding range was much wider. Generally, the fraction found in stand comprised 20% or less, but in some cases, the aboveground fraction was substantially higher, forming up to half the amount in soil (Figure 9). However, in the case of K, the amount bound in biomass was consistently high as compared with the soil pool (Figure 5),

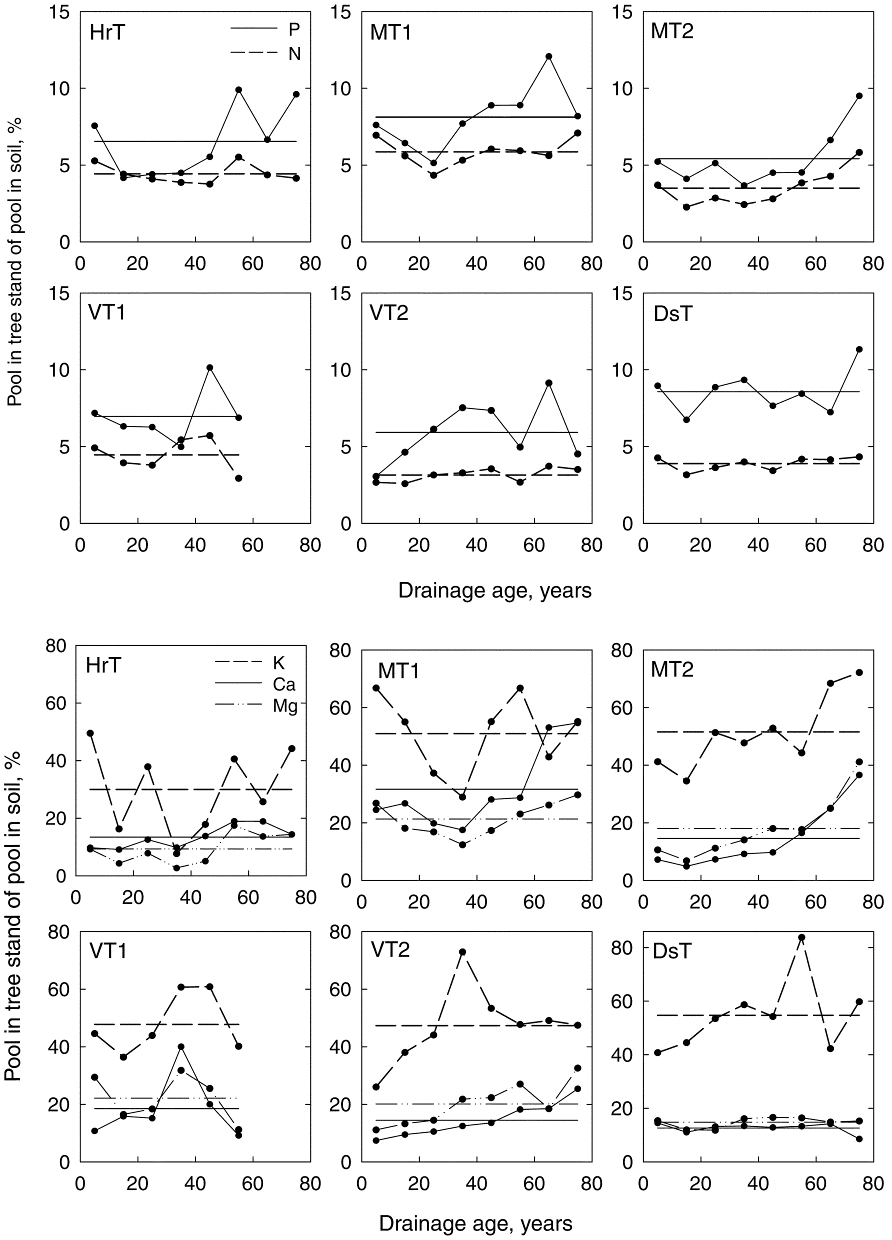

Figure 9. Drainage age class mean values of E_{stand}:E_{soil} ratios (broken lines) in relation to grand means (unbroken lines) across all sites representing a given site type.

and the $\mathbf{E_{stand}}$:$\mathbf{E_{soil}}$ ratios (element pool in tree stand relative to element pool in soil) fluctuated around 50%. Only within HrT was a clearly lower proportion bound in the tree stands (Figure 9).

Over time, within each site type, there tended to be a positive correlation between the $\mathbf{E_{stand}:E_{soil}}$ ratios and time elapsed since ditching (Figure 9), indicating that with time the nutrient pool bound in tree biomass increased relative to the pool in soil. The influence of ditching was most obvious on MT2 and VT2 sites, for which the correlation was significant for N, K, Ca and Mg. Among the nutrients, Ca and Mg most often had an increasing $\mathbf{E_{stand}:E_{soil}}$ ratio. However, in the least fertile DsT site type, the partition between tree stand and soil remained unaffected by the ditching operation. In the case of VT1, scattered data hindered the drawing of conclusions.

Discussion

What does drainage change?

Ditching of peatlands unambiguously influences both stand biomass and structure and, consequently, the nutrient pool bound in trees. Nevertheless, with the exception of Mg, ditching did not markedly decrease soil pools of elements necessary for stand development over the 75-year observation period.

Soil nutrient pools may remain unchanged despite increased tree stand nutrient uptake largely because of compaction of peat soil after drainage, reflected by increases in bulk density (Laiho and Laine 1995; Laiho et al. 1999). The compaction is due to several factors including physical collapse of the pore structure after the water table draw-down, enhanced oxidation processes, gradually increasing weight of the tree stand and accelerated input of tree roots (cf. Minkkinen and Laine (1998a, 1998b)). Because of these processes, the 30-cm peat layers obtained in our sampling are not comparable in a stratigraphical sense across the post-drainage time gradient. The older the drained site is, the more likely the sample core included peat material that was below the 30-cm soil level at the time of drainage.

The soil Mg pool decreased significantly after some decades of post-drainage succession. The same phenomenon has been observed by Laiho and Laine (1995) and Laiho et al. (1999) for site types corresponding to our MT2, VT2 and DsT sites. In their material from a geographically limited area, soil Ca also showed signs of beginning to decrease. In contrast, soil K pool, which generally is considered a critical element on peatlands drained for forestry (Kaunisto and Paavilainen 1988), seems to remain unaffected during the development of the first tree stand generation after drainage (also Laiho and Laine (1995) and Laiho et al. (1999)).

The difference in soil Mg pool between the oldest and youngest drainage age classes for the site types that showed Mg depletion was greater than the corresponding increase in the tree stand Mg pools. Thus, part of the soil Mg has been lost via processes other than tree stand uptake, most obviously through leaching. Moreover, Laiho et al. (1999) concluded that a relatively small part of the estimated Mg (and Ca) lost from soil over 40–60 years following drainage had been accumulated in the tree stand. Indeed, drainage seems to increase the relative leaching rates of Ca and Mg and to reduce that of K (Sallantaus (1992) and unpublished material). In fact, Sallantaus (1992) hypothesized based on hydro-chemical studies that the stores of Ca and Mg in surface peat would diminish already during the first rotation due to leaching losses. The efficient biological cycling, leading to negligible leaching losses of K when in demand by a growing tree stand, has been discussed earlier (Stone and Kszystyniak 1977; Miller et al. 1979). The ability of trees to capture deposition (Schauffler et al. 1996) may be of particular importance to the K economy of drained peatlands (Laiho et al. 1999).

The slight decrease in the base element pool was also reflected in soil acidity and, to a smaller extent, base saturation. Thus, for productive site types, pH decreased when the time span since drainage increased, but on the initially acidic low production sites, drainage had no influence on soil acidity. The most important initial reason for this post-drainage change, and consequently, the primary reason for increased base element leaching is the increased aeration of the surface peat layer, resulting in oxidation of reduced organic carbon and release of hydrogen ions to soil solution (Laine et al. 1995b). Post-drainage increase in nutrient uptake and change in vegetation and litter quality also contribute to soil acidification. Upon drainage, peatland vegetation gradually changes towards upland forest vegetation (Laine et al. 1995a), resulting in formation of a mor-like layer on top of the peat soil (Kaunisto and Paavilainen 1988). These changes induced by drainage would be faster in a warmer climate; correspondingly, soil pH increased with decreasing temperature within most site types.

The increases in the $\mathbf{E_{stand}:E_{soil}}$ ratios unambiguously implied that upon drainage more nutrients are allocated to the developing tree stand or leached from the rooting zone. The former was particularly the case for the composite MT2 and VT2 types, where ditching brought about a shift in tree species composition. Spruce- and birch-dominated sites have on average higher stand volumes than pine-dominated sites. This arises partly from spruce and birch stands generally being situated on more nutrient-rich sites than pine. However, for structural reasons, a Norway spruce also has higher biomass and nutrient content than a Scots pine of the same breast height diameter (Marklund 1988; Finér 1989). According to our estimates, on spruce-dominated sites, some 32% of total aboveground biomass was allocated to needles and branches. In pine and birch stands, the corresponding fraction constituted 24–25%. Thus, the change in tree species composition also had an effect on stand structure and biomass, and consequently, nutrient pools.

Sufficiency of the soil nutrient pools

Generally, for elements like N and P, having large pools in soil relative to tree stand, changes in $\mathbf{E_{stand}:E_{soil}}$ ratios were small, indicating a low risk for future soil pool depletion. For K, with a high amount of total pool bound in biomass, the ratio was in some cases even doubled with increased time since ditching, suggesting a potential future threat of depletion. Only within HrT did the soil K buffer appear adequate, as on these sites a clearly lower proportion was bound in the tree stand, and the partition between soil and biomass was unaffected by ditching. However, since

Table 6. Comparison of nutrient pools in the topmost 30-cm soil layer between mineral soil sites (Westman unpublished and Valmari (1921)) and peatland sites (this study). See text for further detail.

	Upland forest site type[1]			
	CT	VT	MT	OMT
	Drained peatland forest site type			
Source	**DsT**	**VT1+VT2**	**MT1+MT2**	**HrT**
	N, kg m^{-2}			
Westman	0.178	0.184	0.246	0.275
Valmari	0.241	0.263	0.384	0.488
This study	**0.405**	**0.563**	**0.616**	**0.736**
	P, kg m^{-2}			
Westman	0.260	0.345	0.235	0.146
Valmari	0.088	0.111	0.072	0.042
This study	**0.021**	**0.030**	**0.038**	**0.042**
	K, kg m^{-2}			
Westman	0.513	0.291	0.323	0.361
Valmari	0.058	0.060	0.059	0.066
This study	**0.011**	**0.016**	**0.019**	**0.044**
	Ca, kg m^{-2}			
Westman	0.616	0.504	0.655	0.584
Valmari	0.081	0.122	0.137	0.175
This study	**0.065**	**0.092**	**0.118**	**0.211**
	Mg, kg m^{-2}			
Westman	0.887	0.529	0.652	0.603
This study	**0.012**	**0.018**	**0.023**	**0.054**

[1] CT = *Calluna vulgaris* type, VT = *Vaccinium vitis-idaea* type, MT = *V. myrtillus* type, OMT = *Oxalis acetosella - Maianthemum bifolia* type.

K both in peat soils (Starr and Westman 1978) and within the plant (Helmisaari 1992) is a very mobile element even a limited pool may suffice for long time periods if the efficient internal cycling is not disturbed by e.g. tree harvests (cf. also Laiho et al. (1999)). In the case of Ca and Mg, the increase in $\mathbf{E_{stand}:E_{soil}}$ ratios was obvious. Thus, among the base elements, also Ca, which is immobilized in stem wood and removed upon timber harvest, over the long run might become growth-limiting on sites where the tree stand structure is profoundly changed upon ditching. Such depletion of the Ca pool would be in accordance with findings reported by Sallantaus (1992) and Laiho et al. (1999).

A comparison with average soil pools reported for upland forests in Finland (Table 6), gives a further indication of long-term development potential of forests on drained peat soils. Thus, compared to data by Valmari (1921) and Westman (nutrient pool data unpublished, sites described by Liski and Westman (1995)), we found that N pools in peat from forests with a post-drainage development period of 60 years or more were on average substantially higher than in soils from upland sites. Only on DsT sites was the N pool somewhat closer to that of soils from dry and low-production *Calluna* type upland sites.

In the case of N pools, figures are comparable between the three data sets. In all cases, total soil N was determined by Kjeldahl digestion. However, for other nutrients (Table 6), pools as such are not comparable. Westman's data were obtained by digesting the mineral soil samples in strong acid, Valmari's data by extraction with 0.2N HCl and our data by complete hydrolysis of the peat substrate by digestion in strong acids. Consequently, Westman's figures represent soil capacities, while Valmari's figures are nutrient intensities. Thus, Westman's figures for P, K, Ca and Mg are typically higher than those given by Valmari. Our nutrient pools are total amounts, and therefore, capacities like Westman's figures, but since metal elements, such as K and Ca, are highly exchangeable in peat soils (Starr and Westman 1978) these pools also describe intensities. However, when comparing pools in soils from old drained peatlands with those from upland forests, mineral soil pools are clearly much higher. Even in comparison with extractable pools, such as Valmari's intensity values, peat soil pools are generally low. This is particularly the case with the K pool, which except for the most fertile site (HrT) is only 1/4 – 1/5 of the extractable K pool in mineral soils. For P and Ca in peat soils, pools are smaller along low end of our productivity gradient, whereas among the more productive sites, differences compared with extractable pools in mineral soil are inconsistent.

Thus, by the end of a first tree stand rotation, differences in nutrient intensities between mineral soil and peatland sites are not large, except for K, but pools in peat soils are low in terms of capacity. However, since sustainable forestry on peat soils implies a continuous maintenance of a working drainage system, soil development in these sites will continue. During the early years of forest drainage, it was generally assumed that in drained peatlands decomposition exceeds the production of organic matter (e.g. Mikola (1952)), and the rooting zone would thus continuously exploit fresh peat layers, with roots eventually reaching the underlying mineral soil. However, recent findings by Minkkinen and Laine (1998b) and Minkkinen et al. (1999) imply that such development is not always the case. On the more productive sites, i.e. HrT and MTs, decomposition may exceed organic matter input to the soil. On many VTs and DsT, however, net organic matter accumulation to the soil will continue after drainage. Consequently, on these sites the sufficiency of nutrients for forest growth may become an issue over time, unless the influence of ground water flow through the peat deposit, about which we know very little, is significant enough to import nutrients to the rooting zone.

In conclusion, within each peatland site type, the average soil nutrient pool will suffice for the production of at least one post-drainage tree crop. Further, we found little evidence of depletion of soil element pools risking the development of the next tree stand generation. The decreasing trend in the soil Mg pool points on a potential risk in the long run, however.

Potential ability of site type classification for estimating soil nutrient regime of drained peatlands

Water level and the solution pH, which generally reflects soil Ca status, have been found to be the major factors describing the ecological and floristic variation in northern mires (Vitt et al. 1990; Jeglum and He 1995; Wheeler and Proctor 2000). Other factors affecting the vegetation composition include the gradient in fertility related to the limiting nutrients P and N, and the shading effect of the tree canopy (Zogg and Barnes 1995; Bridgham et al. 1996; Wheeler and Proctor 2000). Upon drainage, the hydrological gradient is more or less eliminated and the nutrient gradient gains importance (Laine and Vanha-Majamaa 1992; Laine et al. 1995a).

Varying combinations of pools of single nutrients may support plant communities classified to a given drained peatland site type. Classification to floristic-ecological site types most successfully described soil nutrient status among the most nutrient-poor sites. More than two thirds of DsT sites would be correctly allocated to their respective site type by a linear combination of soil Ca, K, Fe and N pools. MT1 and VT1 were the most heterogeneous site types according to their soil nutrient pools: one quarter of MT1s and slightly more than a third of VT1s would have been recognized on this basis.

When types 1 and 2 were combined within MTs and VTs, masking the original hydrological gradient, soil Ca, P and K pools were the best describers of the productivity gradient (results not shown). In such analysis, on average almost 60% of the floristic-ecological site types correctly reflected soil fertility, and the significance of these element pools agrees with the general view of peat soil fertility. High pools of Ca and other basic (non-hydrolyzing) elements in soil generally imply high productivity, also in upland forest sites (Valmari 1921), and P and K are considered the most likely growth-limiting elements in our peatland forests (Kaunisto 1997; Sundström et al. 2000).

The importance of K, Fe and N pools in the discriminant analysis recognizing all site types was mostly due to their effect in separating types 1 and 2 of VT and MT. This reflects the differences in the hydrological characteristics of these types in the pristine state. Type 1 sites have been relatively dry and well-stocked before drainage, whereas type 2 sites have been wet and sparsely stocked, often with mosaic-like variation in treed ridges or hummocks and treeless depressions.

Consequently, K, which is mostly retained on site by the vegetation, leaches readily from the wet sites with relatively low retention capacity, leading to lower soil K pools in type 2 sites. The higher Fe pools in type 2 sites may be explained by the greater ground water influx to these sites (Solantie 1974) and the precipitation of Fe in peat soils (Puustjärvi 1952). The higher N pools in type 2 sites may be due to higher N_2 fixation by cyanobacteria associated with *Sphagnum* mosses on these moister, less acidic and less shaded sites (Granhall and Selander 1973; Basilier et al. 1978; Waughman and Bellamy 1980). This may significantly affect the total input to soil N pools (Hemond 1983).

As drainage had little effect, the residual variation in soil element pools, not explained by the floristic-ecological site types, would mostly be the result of natural, pre-drainage soil heterogeneity common among pristine peatland site types (Westman 1981). Further, peat depth and temperature sum were identified as significant systematic sources of variation in our material. The residual variation was substantial particularly among the more nutrient-rich site types, which may support many combinations of plant communities. Plant species capable of forming climax plant communities on poorer sites are much fewer in number (e.g. Laine et al. (1995a)).

The significant negative correlation of temperature sum and soil N and P pools within a floristic-ecological site type implies that larger total pools in the rooting zone are required in a colder climate to support a similar plant community structure. This is in accordance with the finding of Sundström et al. (2000) that the ratio between available and total pools of P increased with increasing temperature sum. Thus we may conclude that the floristic-ecological classification of drained peatlands successfully describes their production potential, i.e. nutrient availability, but not their total nutrient pools in varying thermoclimatic conditions.

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Appendix 1

Table A1. Results of the two-way ANOVA on the effects of site type and drainage age on the top 30 cm soil element pools, cation exchange capacity (CEC), base saturation (BS), and pH.

Source	df	N		P		K		Ca		Mg		Mn		Fe		CEC		BS		pH	
		F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p	F	p
Intercept	1	34877.3	< 0.001	6027.3	< 0.001	4574.0	< 0.001	9786.7	< 0.001	3831.2	< 0.001	66.3	< 0.001	3938.1	< 0.001	4198.8	< 0.001	1085.5	< 0.001	17451.4	< 0.001
Site type group (S)	5	26.1	< 0.001	23.0	< 0.001	25.7	< 0.001	27.5	< 0.001	27.1	< 0.001	24.2	< 0.001	29.6	< 0.001	3.6	0.003	11.3	< 0.001	3.1	0.003
Drainage age class (D)	7	0.9	0.493	0.7	0.689	1.1	0.364	1.4	0.224	3.2	0.002	1.3	0.241	3.8	< 0.001	1.2	0.316	1.0	0.454	26.9	< 0.001
S × D	33	0.8	0.835	1.2	0.241	1.2	0.232	0.8	0.774	1.2	0.240	1.5	0.043	1.4	0.063	0.8	0.818	1.0	0.430	1.4	< 0.057
Error	463																				

Table A2. Results of the ANCOVA on the effects of peat depth (thickness of the peat deposit; covariate), effective temperature sum (covariate) and drainage age (fixed factor) on the top 30-cm soil element pools, cation exchange capacity (CEC), base saturation (BS), and pH, for each site type group.

Source	df	HrT		MT1		MT2		VT1		VT2		DsT	
		F	p	F	p	F	p	F	p	F	p	F	p
N													
Intercept	1	98.9	< 0.001	259.0	< 0.001	241.6	< 0.001	240.9	< 0.001	400.8	< 0.001	359.6	< 0.001
Peat depth	1	0.4	0.547	28.5	< 0.001	2.2	0.140	9.2	0.003	6.0	0.016	12.1	0.001
Temp. sum	1	2.2	0.142	< 0.1	0.887	9.3	0.004	0.3	0.587	8.9	0.003	15.0	< 0.001
Dr age	7	0.6	0.789	1.4	0.225	0.6	0.780	1.7	0.154	2.0	0.064	0.7	0.669
P													
Intercept	1	33.6	< 0.001	72.4	< 0.001	117.9	< 0.001	68.0	< 0.001	182.1	< 0.001	180.2	< 0.001
Peat depth	1	4.6	0.037	93.7	< 0.001	8.3	0.006	27.6	< 0.001	21.1	< 0.001	25.4	< 0.001
Temp. sum	1	3.2	0.080	1.2	0.286	18.8	< 0.001	0.1	0.802	16.7	< 0.001	19.5	< 0.001
Dr age	7	1.1	0.367	1.0	0.430	1.3	0.273	0.9	0.477	1.5	0.165	0.8	0.548
K													
Intercept	1	1.6	0.218	39.6	< 0.001	8.5	0.005	38.3	< 0.001	79.0	< 0.001	68.7	< 0.001
Peat depth	1	9.1	0.004	35.3	< 0.001	1.1	0.293	21.8	< 0.001	17.2	< 0.001	9.0	0.003
Temp. sum	1	1.4	0.246	1.2	0.281	3.3	0.076	0.9	0.052	< 0.1	0.915	0.8	0.373
Dr age	7	0.8	0.562	1.2	0.339	1.3	0.259	1.3	0.290	0.7	0.668	1.4	0.197
Ca													
Intercept	1	43.8	< 0.001	41.2	< 0.001	41.0	< 0.001	28.9	< 0.001	56.1	< 0.001	56.4	< 0.001
Peat depth	1	0.6	0.451	0.1	0.709	0.3	0.581	2.5	0.119	0.7	0.399	1.0	0.329
Temp. sum	1	2.9	0.097	0.1	0.770	1.8	0.181	4.5	0.038	0.8	0.358	< 0.1	0.981
Dr age	7	1.1	0.380	1.7	0.115	0.7	0.764	1.4	0.252	1.0	0.456	0.5	0.842
Mg													
Intercept	1	7.8	0.008	34.8	< 0.001	28.2	< 0.001	21.6	< 0.001	46.3	< 0.001	46.9	< 0.001
Peat depth	1	1.7	0.194	19.4	< 0.001	0.1	0.784	0.1	0.703	0.4	0.506	0.2	0.659
Temp. sum	1	0.4	0.546	2.1	0.155	1.8	0.189	0.8	0.386	3.8	0.054	1.0	0.329
Dr age	7	1.1	0.401	1.1	0.351	2.2	0.054	1.2	0.306	2.0	0.064	1.3	0.240

Table A2. Continued.

Source	df	HrT		MT1		MT2		VT1		VT2		DsT	
		F	p	F	p	F	p	F	p	F	p	F	p
Mn													
Intercept	1	18.3	< 0.001	10.5	0.002	4.2	0.046	2.8	0.101	1.3	0.263	7.4	0.007
Peat depth	1	0.4	0.523	5.9	0.018	< 0.1	0.935	3.7	0.060	< 0.1	0.872	< 0.1	0.879
Temp. sum	1	11.5	0.001	4.4	0.040	2.6	0.114	2.0	0.157	0.4	0.507	5.4	0.021
Dr age	7	1.1	0.398	0.3	0.965	1.7	0.125	0.7	0.637	2.2	0.038	0.6	0.793
Fe													
Intercept	1	34.8	< 0.001	53.4	< 0.001	64.4	< 0.001	20.6	< 0.001	74.4	< 0.001	102.1	< 0.001
Peat depth	1	3.2	0.080	12.9	0.001	1.2	0.275	0.7	0.403	2.9	0.092	4.7	0.033
Temp. sum	1	7.2	0.010	9.0	0.004	13.4	< 0.001	0.7	0.414	10.4	0.002	12.2	0.001
Dr age	7	0.9	0.513	1.1	0.373	1.5	0.176	5.6	< 0.001	1.5	0.179	1.5	0.162
CEC													
Intercept	1	9.3	0.004	24.4	< 0.001	1.7	0.203	17.8	< 0.001	16.4	< 0.001	0.5	0.475
Peat depth	1	2.6	0.116	0.3	0.590	0.4	0.543	6.1	0.016	0.1	0.788	3.1	0.080
Temp. sum	1	0.5	0.476	0.4	0.509	1.6	0.210	3.3	0.074	1.2	0.277	20.4	< 0.001
Dr age	7	0.1	0.998	1.5	0.165	0.6	0.744	2.8	0.022	1.6	0.148	0.3	0.937
BS													
Intercept	1	16.8	< 0.001	6.4	0.014	9.2	0.004	9.0	0.004	11.6	0.001	25.5	< 0.001
Peat depth	1	4.7	0.036	14.2	< 0.001	2.4	0.126	13.1	0.001	5.1	0.026	0.8	0.379
Temp. sum	1	8.9	0.005	0.7	0.409	3.5	0.069	0.3	0.564	2.5	0.114	1.2	0.285
Dr age	7	0.5	0.798	1.2	0.300	1.0	0.438	1.2	0.319	1.1	0.352	1.9	0.081
pH													
Intercept	1	72.0	< 0.001	171.5	< 0.001	123.6	< 0.001	206.6	< 0.001	230.1	< 0.001	350.4	< 0.001
Peat depth	1	2.7	0.105	9.2	0.003	< 0.1	0.838	1.3	0.262	< 0.1	0.839	1.2	0.280
Temp. sum	1	17.3	< 0.001	7.2	0.009	16.2	< 0.001	0.4	0.511	16.6	< 0.001	14.6	< 0.001
Dr age	7	1.6	0.155	1.6	0.161	1.2	0.313	2.9	0.019	0.8	0.567	0.6	0.755
Error df		42		75		48		65		104		115	

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