

Foliar Nitrogen, Phosphorus and Potassium Concentrations of Scots Pine in Drained Mires in Finland

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An imbalanced nutrient status in Scots pine stands on drained mires is primarily a consequence of excess nitrogen (N) in relation to mineral nutrients such as phosphorus (P) and potassium (K). In this study, the variation of foliar N, P, and K concentrations relative to some site and environmental characteristics was examined. Foliar nutrient concentrations were determined on needle samples collected from mires representing different drainage ages, site types, geographical locations and annual weather conditions. In the overall data ($n = 971$ samples in 333 stands) the foliar N concentration varied between 6.7 and 24.2 mg g⁻¹, the P concentration between 0.83 and 2.32 mg g⁻¹, and the K concentration between 2.22 and 6.23 mg g⁻¹. The original (pre-drainage) mire site type proved to be an important factor in explaining the nutrient status of the trees: on originally forested sites, the nutrient balance (N versus K; N versus P) was mostly adequate, whereas on sparsely forested and treeless sites, K deficiency was common. N deficiency was the most common in forested 'nitrogen-poor' sites, while P and K deficiencies were more common in originally treeless or sparsely forested 'nitrogen rich' sites, where the nutrient imbalance was also the greatest. Over the whole data, 29% of the cases were diagnosed to be N-deficient, 51% P-deficient, and 25% K-deficient. The foliar N concentration increased with increasing temperature sum. The foliar K concentration decreased with increasing depth of the peat layer. On former treeless or sparsely forested sites, foliar K decreased slightly with increasing drainage age. In contrast, on thin-peated sites the foliar P concentration increased with increasing drainage age. The climate conditions (location), the original site type of the mire and peat thickness should be taken into account when planning silvicultural measures on mires drained for forestry.

Keywords peatland, drainage, site type, nutrient deficiency, foliar analysis

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1 Introduction

On pristine mires the conditions for tree growth are generally unfavourable compared with those on upland forests. Owing to the persistent high water table level and fluctuations in water-saturated anaerobic conditions, the aeration in the rooting zone is insufficient for trees. Excessive water also prevents microbial activity and decomposition in the peat substrate. Therefore, drainage is in most cases a prerequisite for economic wood production on peat soils.

During the latter part of the last century, drainage was utilized in a large scale in the Nordic countries, the British Isles, Russia, the Baltic states and in some regions in North America (Haavisto and Jeglum 1991, Paavilainen and Päivänen 1995). The objective of forest drainage is to lower the water table to a level that improves soil aeration in the trees' root system. The enhanced supply of oxygen increases the bacterial biomass and further intensifies the mineralization of plant nutrients (Lähde 1966, Karsisto 1979, Lieffers 1988, Silins and Rothwell 1999).

Finland is home to one third of the world's 15 million hectares of mires drained for forestry. About 5.5 million hectares were drained for forestry during the past century (Hökkä et al. 2002). It has been estimated that the current annual tree growth on all peatlands (24 mill. m³ yr⁻¹) now accounts for about one quarter of the total growing stock of all forest land in Finland. This is approximately three times the total tree growth of peatlands in the 1950s (Tomppo 2005).

Initially, drainage was carried out primarily on naturally forested sites but, as it became mechanized during the 1950s and 60s, it was expanded to open fens and thick-peated oligotrophic bogs. In such sites, stand yield is limited by a shortage or imbalance of nutrients in the growing substrate (Keltikangas et al. 1986). Therefore, fertilization has been carried out widely – one third (1.6 mill. ha) of the total drainage area has received PK or NPK fertilizer.

In contrast to mineral forest soils, peat contains an abundance of nitrogen (N), but a low amount of mineral nutrients. However, there is considerable variation in nutrient amounts within and between site types (Westman and Laiho 2003)

and, in recent studies, considerable peatland-basin and region-level variation has also been reported (Laiho et al. 2008).

Nitrogen is mainly present in peat in the form of organic nitrogen, which is not directly available to plants. There is considerable variation in the N availability of trees between sites, depending e.g. on the peat type (*Carex* vs. *Sphagnum*), total N concentration in the peat and peat temperature (Pietiläinen and Kaunisto 2003, Hartman et al. 2003, Potila and Sarjala 2004). In general, the total amount of N in surface peat is sufficient to meet the requirements of the trees on most site types (Laiho and Laine 1994, Westman and Laiho 2003). Owing to the slow N mineralization rate, however, trees growing on oligotrophic drained mires may suffer from a low availability of nitrogen (Kaunisto 1977, Kaunisto and Paavilainen 1977, Moilanen and Issakainen 1990). The scarcity of nitrogen limits tree growth, particularly during cold growing seasons (Westman 1979, Hytönen and Silfverberg 1991, Sundström et al. 2000). Excessive amounts of N – especially when the availability of K or B is low – can cause physiological problems such as growth disturbances and decreased cold resistance (Aronsson 1980, Ferm et al. 1990).

The main source of potassium (K) for plants is the weathering of soil minerals. Potassium stocks in peat are very low compared to those in mineral soil (Westman and Laiho 2003). A shortage of K is the most common on thick-peated, originally sparsely forested or treeless sites (Kaunisto and Tukeyva 1984), where equal or even higher amounts of K can be bound in the tree stand than in the 0–20 cm surface peat layer (Laiho and Laine 1995, Moilanen et al. 1996, Kaunisto and Moilanen 1998). Consequently, there is a risk of future depletion of the K pool after tree harvesting (Kaunisto and Paavilainen 1988). Both the K in the soil solution and that bound on humus colloids in peat is freely available, or only weakly bound to cation exchange sites as K⁺. Potassium is readily available and efficiently fixed in living trees but, as a mobile element, it is also leached easily (Ahti 1983, Kaunisto 1992, Malcolm and Cuttle 1983, Wells and Williams 1996). Although the ratio between the amount of K in a tree stand and that in the soil has, in some cases, even doubled following ditching, it has not always been possible to

detect a reduction in K stocks even in old drainage areas (Laiho and Laine 1994, Laiho et al. 1999, Westman and Laiho 2003). The thickness of the peat deposit may, in the long run, play a decisive role in the development of K status in the tree stand. The compaction and settling of peat over time may result in an improved K status, especially on thin-peated sites, where the root system is able to reach the underlying mineral subsoil (Moilanen et al. 1996, Saarinen 1997).

Most of the phosphorus (P) in peat is bound in organic matter and as occluded iron (Fe), aluminium (Al), and calcium (Ca) phosphate (e.g. Kaila 1956, Nieminen and Jarva 1996, Nieminen and Penttilä 2004). The total phosphorus pool in the surface peat is large in relation to the potassium pool, as well as to the amount accumulated in the tree stand (Westman and Laiho 2003), but mineralization into an available form due to microbial activity is often slower than the tree would require. The ratio between N and P pools in peat is generally higher than in trees. When peat N and P are released by microbes in the same ratio (Alexander 1967), it often results in a shortage of available P compared to available N.

The changes in soil nutrient pools during at least one post-drainage rotation are minor, despite increased nutrient uptake by the tree stand (Westman and Laiho 2003). In fact, drainage may lead to increases in the amounts of N and P in the rooting zone due to compaction (increased bulk density) of the surface peat (Kaunisto and Paavilainen 1988, Laiho and Laine 1994, Laiho et al. 1999). On the other hand, the calcium (Ca), potassium (K), magnesium (Mg), boron (B) and zinc (Zn) stocks may remain at approximately the same level as those in the surface peat of undrained mires. However, they may also diminish due to leaching and to uptake by the vegetation (especially the tree stand) (Kaunisto and Paavilainen 1988, Laiho and Laine 1995, Sundström et al. 2000).

Nutrient deficiencies and imbalances in trees have been reported especially on thick-peated, originally treeless or sparsely forested sites dominated by mesotrophic and oligo-mesotrophic *Carex*-dominant site types (Silver and Saarinen 2001, Pietiläinen et al. 2005, Silfverberg and Moilanen 2008). Low levels of P and K and the considerable effects of fertilizers on stands suffer-

ing from deficiencies have been verified in numerous studies in Finland during the last decades (e.g. Paarlahti et al. 1971, Moilanen 1993, Silfverberg and Hartman 1999).

A more specific understanding of the relationship between soil and tree stand nutrition in different site types has so far not been reached, and present-day knowledge is insufficient for evaluating the sustainability of nutrient stocks for long-term wood production. There is still a lack of knowledge about the nutritional differences between originally forested sites, sparsely forested and open treeless site types. Studies comparing the variation in the nutrient status of trees growing on different mire site types, in various parts of the country or in different climate regions, are rare (see, however, Silfverberg and Moilanen 2008). More precise knowledge on the development of the post-drainage nutrient regime would offer useful tools for management planning of practical forestry. More precise guidelines are needed for choosing sites for profitable remedial drainage operations and fertilization.

The aim of this study is to clarify and model the variation in the nutrient regime of Scots pine growing on drained mires in terms of N, P and K. The nutrient status was evaluated through foliar nutrient diagnosis. The main focus was on identifying stand characteristics (drainage age, site type, peat thickness) or environmental factors (geographical location, weather conditions) that would explain the variation in nutrient concentrations. It was hypothesized that:

- 1) A shortage of K is more prevalent and that of N less prevalent in stands transformed from open treeless or sparsely treed mires than on sites that were originally forested before drainage.
- 2) The foliar N concentration is related to the temperature sum of the birth year of the needles.
- 3) N deficiencies are common, and P and K deficiencies uncommon, in thin-peated sites (peat deposit < 40 cm), while in thick-peated sites the situation is the opposite.

2 Material and Methods

2.1 Experiments

The data were compiled from needle nutrient analyses that had been carried out on experimental stands on drained mires established and monitored by Metla (Finnish Forest Research Institute). Needle analysis is a frequently used method for monitoring the nutrient status and nutrient imbalances of trees in practical forestry. Nutrient concentrations of living, current needles reflect the nutrient status of the trees and are important indicators of tree growth and soil productivity (e.g. Moilanen 1993, Pietiläinen and Kaunisto 2003, Korkalainen et al. 2007, Silfverberg and Moilanen 2008). In Finland, needle analysis has been widely used in studies on the nutrient requirements and deficiencies of Scots pine on drained mires (e.g. Paarlahti et al. 1971, Kaunisto 1987, Moilanen 1993, Hytönen and Kokko 2006).

The oldest experiments had been established in the early 1960s and the youngest in the late 1990s. An experimental stand generally consisted of 10–40 sample plots, including 3–4 treatments (fertilization, thinning). The size of the individual sample plots varied from 0.09 to 0.15 ha. In this study, only the unfertilized and unthinned plots were utilized. The total material included 333 experimental stands.

The majority of the stands were located in the Southern boreal aapa mire zone (Ruuhijärvi 1983), specifically in the area of Muhos municipality nearby Oulu. The northernmost experimental stands were located ca. 100 km above the Arctic Circle in the Northern boreal aapa mire zone. The southern and westernmost stands were located in a zone of eccentric bogs, and the easternmost stands in the Southern boreal aapa mire zone near the Russian border (Fig. 1).

Background information on the experimental sites (site type, drainage information, time of cuttings) was collated from Metla's archives, establishment documents and previous publications. The following information was available for every experiment: 1) location (coordinates) and elevation above sea level (m), 2) the original mire site type (forested, sparsely forested, tree-

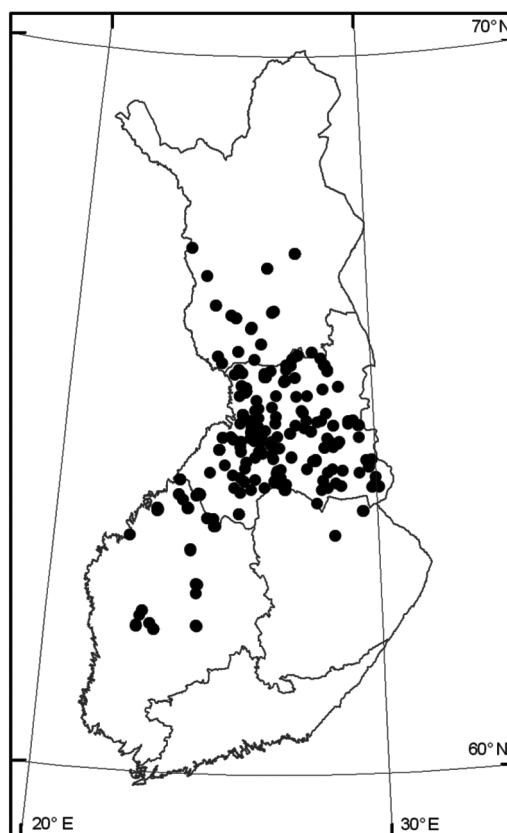


Fig. 1. Location of the experimental stands (n = 333).

less) (according to Vasander and Laine 2008), 3) site fertility type (eutrophic, herb-rich, tall-sedge, low-sedge, dwarf-shrub/cottongrass, *Sphagnum*) (according to Huikari 1952), 4) the depth of the peat layer (cm, maximum value 100), 5) mean stand height (m), and 6) time elapsed between initial drainage or ditch maintenance and needle sampling (years) (Table 1).

Most of the experiments were first drained in the 1960s and 70s. On average, 33 years (ranging 1–85 years) had elapsed between the first drainage and needle sampling. Ditch maintenance draining had been carried out during the 25 years after the first drainage in most of the stands. The drainage efficiency was thus assessed to have remained good or satisfactory during the study period. More than 10 years had passed since any silvicultural treatment (e.g. thinning) in all cases. The dominant tree species was Scots pine (*Pinus*

sylvestris L.) with minor admixtures of downy birch (*Betula pubescens* Ehrh.) and/or Norway spruce (*Picea abies* (L.) Karst.) (5–25% of the stem volume). The mean height of Scots pine varied between 3–19 m, depending on the experiment. Only 15% of the experimental stands were thin-peated (depth of the peat layer less than 30 cm). Half (51%) of the stands were on sites with a peat layer depth exceeding one meter. There was considerable variation between the study sites as regards the effective temperature sum, owing to geographical and annual variation. The warmest summer was almost two times warmer than the coolest summer (Table 1).

2.2 Needle Sampling and Chemical Analysis

Altogether 971 needle samples were collected from 333 stands in 1973–2003 for nutrient analysis. Around one fourth (23%) of the samples were

from originally forested mire site types, mostly oligotrophic and ‘nitrogen-poor’ sites (see Vasander and Laine 2008; referred to as ‘forested’ later in the text). The majority (53%) were from former sparsely forested mixed mire site types, which are mostly oligo-mesotrophic and ‘moderate nitrogen-rich’ sites and characterized by a mosaic of hummock-lawn-hollow vegetation (‘sparsely forested’). One quarter (24%) was from former open and treeless ‘nitrogen-rich’ site types (‘treeless’) (Table 2). The most common site fertility types (for classification see Huikari 1952) were low-sedge and tall-sedge types (37% and 31%, respectively). The cottongrass type accounted for 25% and the herb-rich type for 6% of all the samples. The most fertile (eutrophic) and the least fertile (*Sphagnum*) site types were both represented by less than 10 samples.

The number of sampled plots in an experimental stand varied between 2 and 5. One needle sample was taken from each plot in the stand, and consisted of needles from 6–8 trees per plot. 1–2 current lateral shoots, formed in the previous summer, were taken from each tree. The branches were collected with a branch cutter from the southern side of the upper third of the living crown. Samples were not collected from trees growing near (< 3 m) the ditches. The samples were collected in winter time – during the dormant period of the trees – as recommended (Paarlahti et al. 1971, Reinikainen et al. 1998), when the fluctuation in nutrient concentrations is at its minimum (e.g. Tamm 1955, Helmissaari 1990).

The N concentration was determined spectrophotometrically (salicylate method) on the needle samples digested by the Kjeldahl method, as

Table 1. Summary of the site characteristics of the 333 stands.

	Minimum	Mean	Maximum
Longitude	22°	26°	30°
Latitude	62°	65°	67°
Elevation (m a.s.l.)	15	105	270
Temperature sum ^a , d.d.	699	1033	1339
Peat thickness (cm) ^b	2	>75	>100
Mean stand height (m) (Scots pine)	3	7.1	19.0
Years from drainage	1	33	85

^a Effective temperature sum (threshold value +5°C) for the growing season when the needles appeared; ^b the range in peat thickness measurement was 2–100 cm.

Table 2. Number of needle samples by original mire site type and site fertility type group.

Site fertility (Huikari 1952)	Original mire site type (Vasander and Laine 2008)			Total
	Forested	Sparsely forested	Treeless	
Eutrophic	–	3	1	4
Herb-rich	–	30	25	55
Tall-sedge	4	222	77	303
Low-sedge	166	150	40	356
Dwarf-shrub/cottongrass	45	109	90	244
<i>Sphagnum</i>	5	–	4	9
Total	220	514	237	971

outlined by Halonen et al. (1983). After dry combustion and extraction with hydrochloric acid (HCl), the K concentration was determined using an atomic absorption spectrophotometer (AAS) and the P concentration using the vanado-molybdate method (Halonen et al. 1983). Some of the analysis results have already been published by experiment or experiment group in earlier studies (e.g. Moilanen 1992, 1993, Kaunisto et al. 1999, Moilanen et al. 2005, Pietiläinen et al. 2005).

Interpretation of the needle analyses is based on previous research and on recommendations concerning the deficiency limits and optimal concentrations of nutrients. The following concentrations (mg g⁻¹) for poor, adequate and optimal nutrient status of Scots pine (Paarlahti et al. 1971, Reinikainen et al. 1998) were used in the interpretation:

Nutrient	Poor	Adequate	Optimal
N	< 12	12–13	13–18
P	< 1.3	1.3–1.6	1.6–2.2
K	< 3.5	3.5–4.5	4.5–5.5

The ratios between the N, P and K concentrations are also important measures when estimating the nutrient status and growth potential of a tree stand. It has been suggested that the optimal N:P ratio would be about 11, and the optimal N:K ratio about 3.5 (Puustjärvi 1962a, 1962b).

2.3 Data Analysis

Correlation analysis was first used to clarify the relationships between the measured site characteristics and the foliar nutrient concentrations. Differences in the foliar N, P, K, N:P ratio and N:K ratio between site fertility type groups and between original mire site type groups were tested with a one-way analysis of variance model. The statistical significance of the differences among the groups was analyzed using the Bonferroni paired t-test.

A general linear mixed model was then constructed to study the dependence of the foliar N, K and P concentrations on site and environmental characteristics. For this purpose, the original data (971 nutrient analyses) were divided into

two groups: dataset A (n = 467), which included those sites with a measured peat thickness ranging from 5 to 100 cm, and dataset B (n = 601), which included those mixed and treeless mire types with a peat thickness of 50–100 cm, as well as all the remaining sites of any type where the total peat thickness had not been measured but where it was at least 100 cm. The purpose of dataset A was to construct the model in two phases, starting with fitting peat thickness and site type into the model. Testing began with the hypothesis that *peat thickness* and pre-drainage *hydrology and tree density* are the most important factors affecting the needle K concentration. In delimiting dataset B, existing reports (e.g. Silfverberg and Moilanen 2008) about K and P deficiencies being concentrated on thick-peated and originally wet and partly open mire types was used. The minimum peat thickness used, 50 cm, was also partly based on the test results gained from dataset A. Thus, the purpose of dataset B was to focus on only those site types that commonly suffer from a lack of nutrients and nutrient imbalances, and to test the effect of *geographical location and drainage age* on the variation in nutrient status.

Because of the hierarchical data structure, with two random levels (block and plot) and with site and environmental factors as fixed effects, a general linear mixed model (SAS mixed procedure) was applied:

$$y_{ij} = \beta_0 + \beta x_{ij} + u_j + \varepsilon_{ij} \quad (1)$$

where y_{ij} is the dependent variable and β_0 a constant. The fixed part of the model contains independent variables x_{ij} , that are either on the experimental stand (block) level (temperature sum, drainage age, altitude) or on the plot level (peat thickness, stand height, mire site type) with parameter β (Searle 1987). The random part includes random block effect u_j (experimental stand) and the normally distributed error, ε_{ij} (plot). The random factor defined blocks (experimental stands) as being independent of each other, but the internal covariance structure of the block was in compound symmetry. As a result, the correlations of every plot to the response variable were made equal within each experiment.

The weather conditions in the experimental stands were derived with models based on the

Table 3. Mean foliar N, P, and K concentrations (standard error in parentheses) by original site type and site fertility type with the F-values of variance analysis. Differences between the values marked with the same letters are not statistically significant within the nutrient according to Bonferroni test ($p > 0.05$). The classes 'eutrophic' and '*Sphagnum*' were excluded from the analyses because of the small number of observations.

	Forested	Sparsely forested	Treeless	
Original mire site type (n = 958)				
N, mg g ⁻¹	12.0 a (0.011)	13.3 b (0.001)	14.9 c (0.020)	
P, mg g ⁻¹	1.41 a (0.016)	1.34 b (0.011)	1.20 c (0.016)	
K, mg g ⁻¹	4.34 a (0.038)	3.99 b (0.030)	3.67 c (0.037)	
N:P ratio	8.7 a (0.109)	10.3 b (0.123)	13.0 c (0.265)	
N:K ratio	2.8 a (0.038)	3.4 b (0.039)	4.2 c (0.079)	
	Herb-rich	Tall-sedge	Low-sedge	Dwarf-shrub-cottongrass
Site fertility type (n = 958)				
N, mg g ⁻¹	15.3 a (0.043)	14.1 b (0.016)	12.7 ce (0.011)	13.1 de (0.012)
P, mg g ⁻¹	1.26 a (0.026)	1.32 a (0.016)	1.38 b (0.014)	1.25 ac (0.014)
K, mg g ⁻¹	3.6 a (0.064)	3.9 a (0.041)	4.1 bd (0.036)	4.1 cd (0.040)
N:P ratio	12.6 a (0.561)	11.3 ac (0.225)	9.5 b (0.135)	10.8 bc (0.177)
N:K ratio	4.3 a (0.139)	3.8 b (0.665)	3.2 c (0.048)	3.3 c (0.054)

geographical location and elevation above sea level (Ojansuu and Henttonen 1983). The models were used to calculate the effective temperature sum (day-degree sum; threshold +5°C) for the growing season when the needles first appeared. The climatological data – compiled from the measurements made by the Finnish Meteorological Institute – included variation both between location (north–south) and between different years.

3 Results

3.1 Nutrient Status of the Trees

Foliar nutrient concentration range in the whole data was for N 6.7–24.2 mg g⁻¹, for P 0.83–2.32 mg g⁻¹ and for K 2.22–6.23 mg g⁻¹. Significant differences were found in the nutrient concentra-

tions among the original site types and fertility types (Table 3). The highest N values were found on treeless sites and the lowest on forested sites. The situation as regards P and K was the opposite. As regards fertility types, the highest foliar N values were found in the “fertile” herb-rich class and the lowest in the “barren” low-sedge and dwarf-shrub/cottongrass classes. The highest K concentrations occurred on the sites classified as low-sedge and dwarf-shrub/cottongrass groups. Differences in the N:P and N:K ratios between the original mire site type groups were significant, too.

The overall nutrient status of the tree stands was: 49% of the samples indicated a severe P shortage, 29% a N shortage and 25% a K shortage. Simultaneous P and K deficiency occurred in 18% of the samples and simultaneous N, P and K deficiency in 4% of the samples. There were considerably more cases of N deficiency on

the forested sites than on the treeless or sparsely forested sites (55%, 27% and 18% of the samples, respectively). The situation for K was the opposite: the proportion of needle samples with a foliar K concentration below 3.5 mg g⁻¹ was 9% (forested), 26% (sparsely forested) and 40% (treeless). Likewise, P deficiencies were more common on treeless sites (71%) than on the sparsely forested or forested sites (50% and 38%).

Some significant correlations ($p < 0.000$) were found between the foliar nutrient concentrations and the site characteristics. The concentration of N correlated positively with the temperature sum of the growing season when the needles appeared ($r = 0.222$), and with the peat thickness ($r = 0.284$). The foliar K concentration correlated negatively with peat the thickness ($r = -0.277$) and drainage age (-0.242). The relationship between stand height and the nutrient concentrations was non-significant.

3.2 Factors Explaining the Variation in Foliar N, P and K Concentrations

The original mire site type significantly explained the variation in the foliar N concentration (Table 4). However, the differences between site types varied depending on the temperature sum. Significant interaction were found between site type and temperature sum, suggesting that there was a trend of increasing foliar N concentration with increasing temperature on the forested and sparsely forested sites, but not on the treeless mires. The second order interaction among peat thickness, site type and temperature sum indicated that there was an increasing foliar N concentration with increasing peat thickness on the sparsely forested sites, but not in the other site types (Fig. 2). In shallow-peated sites the highest N values occurred in originally treeless mires, whereas on deep-peated sites the highest N values were found in sparsely forested mires.

On thick-peated sites (peat deposit more than 50 cm) the main effect of altitude on the foliar N concentration was significant, as was the interaction between the altitude and temperature sum (Table 5). The decreasing trend in foliar N with increasing altitude was the more stronger, the higher the temperature sum (Fig. 3). On the aver-

Table 4. Models for predicting the foliar N, P, and K concentration of Scots pine on the basis of certain site characteristics (dataset A, $n = 467$). Peat_d = peat thickness; Temp = temperature sum of growing season when the needles first appeared; Age_d = years from drainage; Site = original mire site type; Alt = altitude (above sea level).

Factor	F-value	NumDF	DenDF	p-value
Nitrogen (N)				
Site	6.31	2	398	0.0020
Site* Temp	4.43	3	336	0.0045
Site * Temp*Peat _d	3.97	3	422	0.0082
Phosphorus (P)				
Site*Temp*Age _d	6.29	3	344	0.0004
Site*Temp*Age _d *Peat _d	4.05	3	411	0.0075
Potassium (K)				
Site*Peat _d *Temp	15.10	3	399	<0.0001
Site* Aged	7.07	3	267	0.0001

Table 5. Models for predicting the foliar N, P, and K concentration in Scots pine on the basis of certain site characteristics (dataset B, $n = 601$). Age_d = years from drainage; Temp = temperature sum of growing season when the needles first appeared; Alt = altitude (above sea level).

Factor	F-value	NumDF	DenDF	p-value
Nitrogen (N)				
Alt	17.47	1	303	0.0016
Alt * Temp	16.82	1	298	0.0322
Phosphorus (P)				
N*Temp	14.54	1	608	0.0002
Potassium (K)				
N	17.58	1	449	<0.0001
N* Age _d	16.06	1	422	<0.0001
N*Temp	21.10	1	413	<0.0001
N*Age _d * Temp	12.04	1	428	0.0006
N*Age _d *Alt	5.94	1	245	0.0155

age, foliar N increased with increasing temperature sum.

As regards foliar P, the significant second order interaction among site type, drainage age and temperature sum suggested that the P concentration increased with increasing drainage age only on originally forested sites, and this interaction

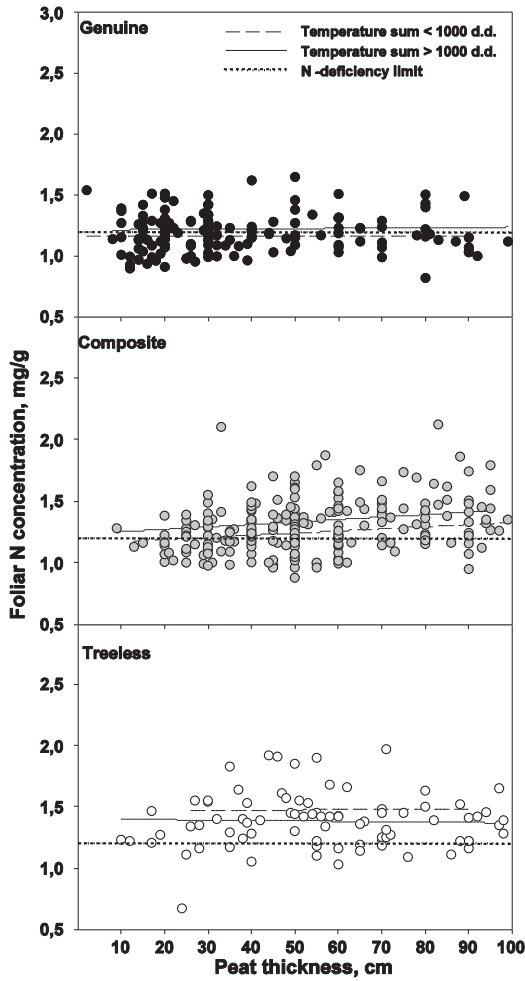


Fig. 2. Relationship between foliar N concentration, peat thickness, site type and temperature sum (dataset A, n = 467). Genuine = originally forested site, composite = sparsely forested site, treeless = originally treeless site.

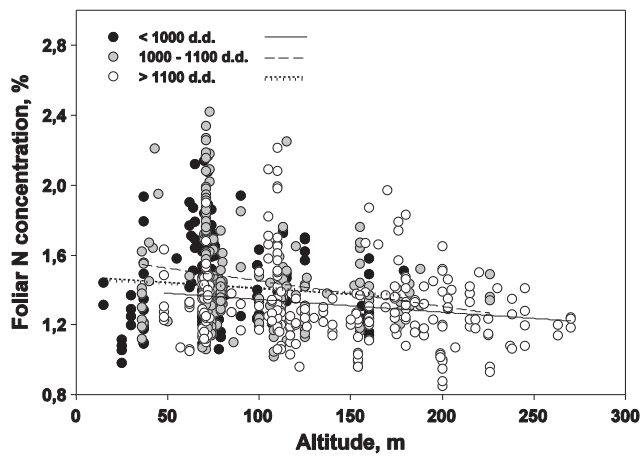


Fig. 3. Relationship between foliar N concentration, altitude and temperature sum. Thick-peated sites (dataset B, n = 601).

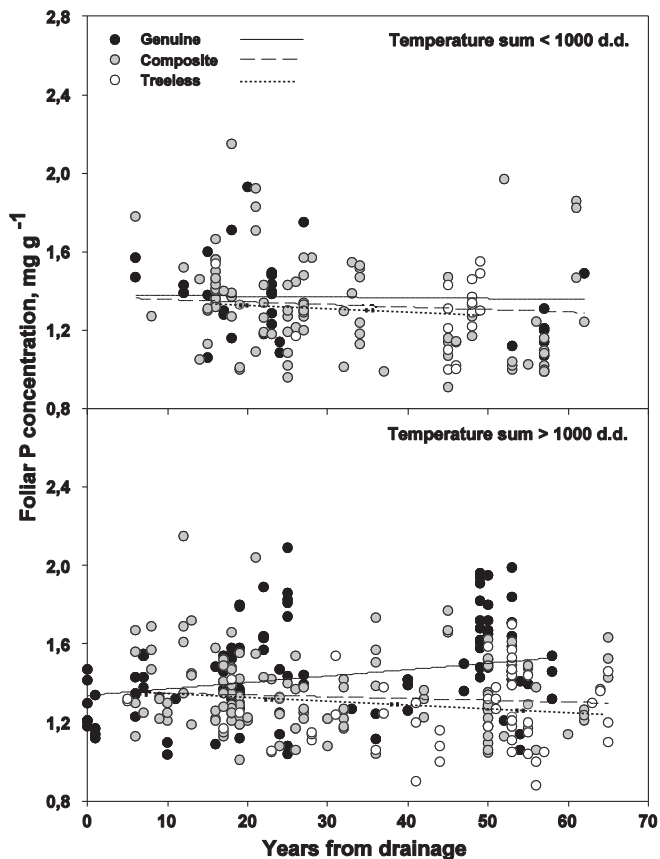


Fig. 4. Relationship between foliar P concentration, drainage age, site type and temperature sum (dataset A, n = 467). Genuine = originally forested site, composite = sparsely forested site, treeless = originally treeless site.

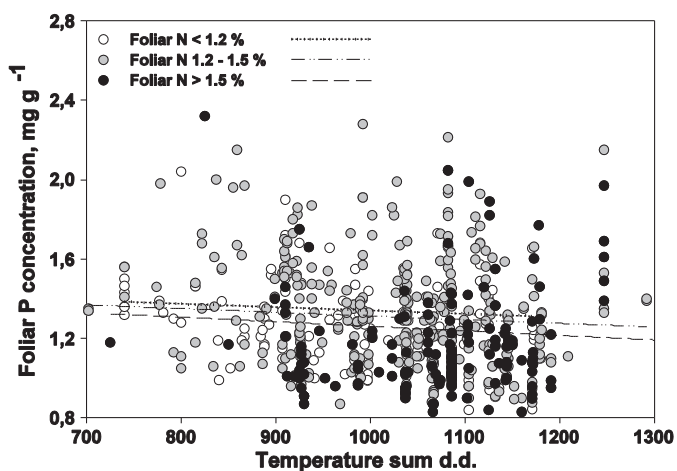


Fig. 5. Relationship between foliar P concentration, temperature sum and foliar N concentration. Thick-peated sites (dataset B, n = 601).

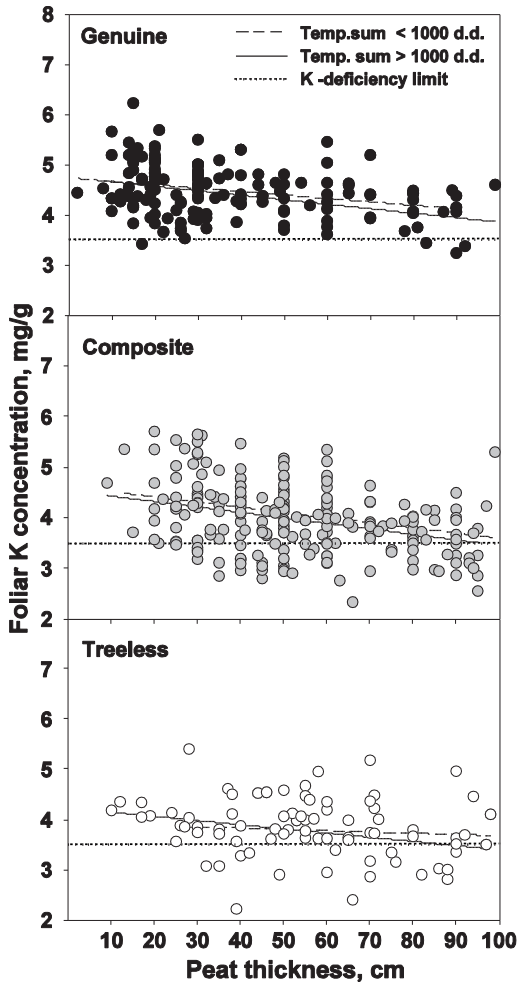


Fig. 6. Relationship between foliar K concentration, peat thickness, temperature sum and site type (dataset A, n = 467). Genuine = originally forested site, composite = sparsely forested site, treeless = originally treeless site.

was true only on sites with a high temperature sum (Table 4, Fig. 4). Moreover, the third order interaction (Site*Temp*Age_d*Peat_d) suggested that the above-mentioned second order interaction only occurred on the sites where the peat thickness was less than 50 cm. This means that the originally forested and oldest drainage areas on shallow peat layers and in relatively warm climatic conditions had the highest P concentrations. On thick-peated sites, where the roots cannot

penetrate into the underlying mineral soil, there was a significant interaction among temperature sum and the foliar N concentration (Table 5), indicating that the decreasing trend of the P concentration with increasing temperature sum was the most pronounced on sites with high foliar N concentrations (Fig. 5).

The foliar K concentration increased with decreasing peat thickness, especially on originally forested sites and sparsely forested sites (significant interaction among site type and peat thickness) (Table 4, Fig. 6). The strength of this connection depended on the temperature sum: on originally treeless sites, the effect of peat thickness decreased with decreasing temperature sum, whereas on the sparsely forested sites the effect was independent of the temperature sum. Significant interaction among drainage age and site type indicated that there was a decreasing trend in foliar K concentration with increasing drainage age on sparsely forested sites and especially on treeless sites (Fig. 7).

Because the foliar N concentration was dependent on the altitude and temperature sum (Fig. 3, Table 5), and also negatively correlated with foliar K, it was assumed to be a significant factor among drainage age, temperature sum and altitude when explaining the variation in foliar K on thick-peated sites. This can be seen from Table 5, which shows a significant interaction between drainage age and foliar N. However, this interaction was dependent on both the temperature sum and altitude, thereby expressing significant second order interactions, respectively (N*Age_d*Temp and N*Age_d*Alt). The former interaction (N*Age_d*Temp) indicated that foliar K concentration decreased with increasing drainage age and increasing foliar N concentration especially in cool climatic conditions (Fig. 8). On the average, the higher the N concentration, the lower was the foliar K concentration. The second order interaction among foliar N, drainage age and altitude indicates how the interdependence between foliar K and altitude was dependent on the drainage age and foliar N (Fig. 9). An increasing foliar K concentration and increasing altitude coincided especially in young drainage areas. In older drainage areas altitude had an increasing effect on foliar K concentrations only in connection with lower foliar N concentrations.

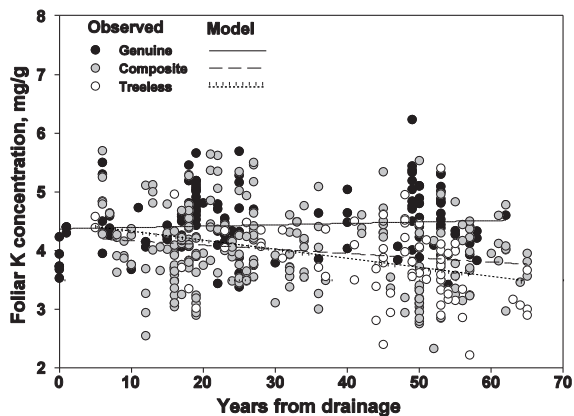


Fig. 7. Relationship between foliar K concentration, drainage age and site type (dataset A, n = 467). Genuine = originally forested site, composite = sparsely forested site, treeless = originally treeless site.

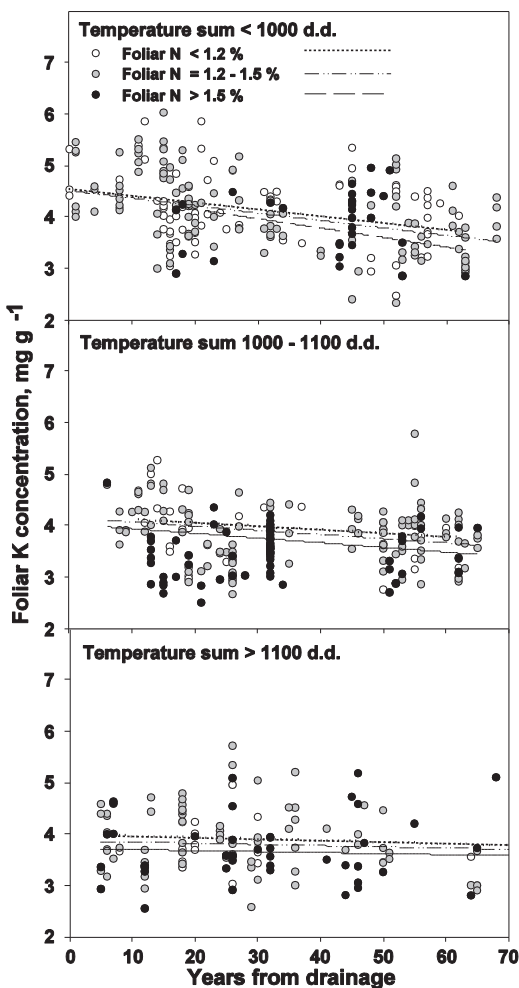


Fig. 8. Relationship between foliar K concentration, drainage age, temperature sum and foliar N concentration. Thick-peated sites (dataset B, n = 601).

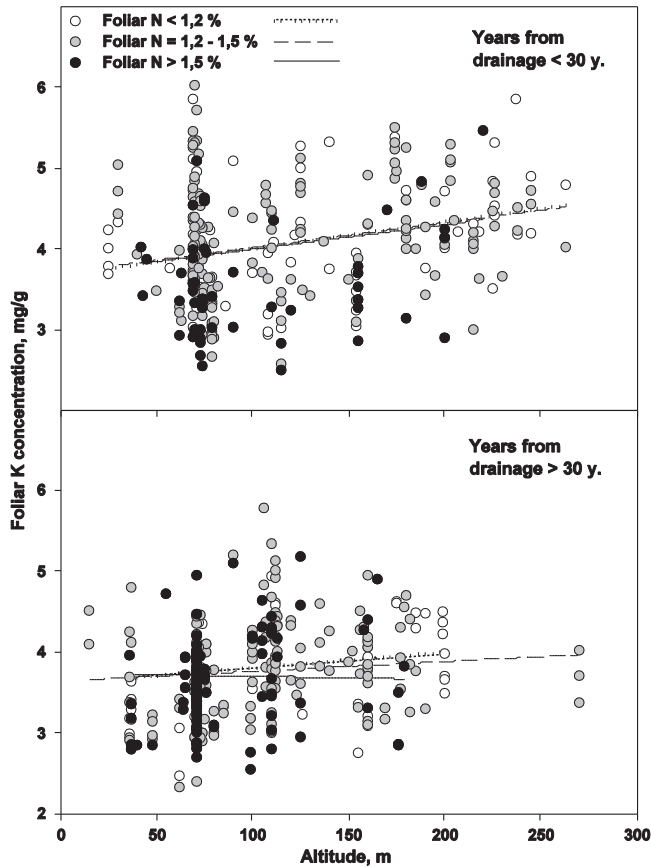


Fig. 9. Relationship between foliar K concentration, altitude, drainage age and foliar N concentration. Thick-peated sites (dataset B, n=601).

4 Discussion

4.1 Representativeness of the Data

The material consisted of nutrient analyses from Scots pine needle samples collected in different years and site types across the country. The aim was to elucidate the factors affecting the nutrient status of Scots pine growing on drained mires. No corresponding study has earlier been carried out.

All the most important mire fertility types – which have been common drainage targets in practical forestry (Keltikangas et al. 1986) – were sufficiently represented in the material. Moreover, the data also included considerable variation in

climatic conditions (between the northernmost and southernmost experiments), as well as years with considerably different temperature conditions. However, the geographical distribution of the stands was uneven, and covered only a minor part of Finland. Most of the experimental stands were located in Central Finland. The relative lack of data from Southern Finland limits the applicability of the results to the whole of Finland. Thus, the results best represent the peatland complex type in the Southern boreal aapa mire zone (Ruuhijärvi 1983). Variation in the nutrient concentrations was considerable, and represented the whole range of variation limits reported for Scots pine (Reinikainen et al. 1998). Many of the previous studies on nutrient status have been

restricted to nutrient deficient stands only (e.g. Kaunisto and Tukeva 1984, Moilanen 1993, Rautjärvi et al. 2004, Moilanen et al. 2005, Pietiläinen et al. 2005). The stands included in the present study represent a wide range of nutrient statuses, not just “good” or “poor.”

The analyses were performed over a long period of time in different Metla laboratories. It is therefore possible that, despite the use of standard analysis methods, there might be some systematic temporal trends in the foliar nutrient concentrations due to e.g. differences in the analytical instruments used. This uncertainty and possible source of systematic error should certainly be taken into account, especially when examining the long-term developments in the nutrient status of the trees. However, during sampling, care was taken to target similar sites each year as regards site fertility, peat thickness, etc. Therefore, we consider that any possible bias due to differences in methodology or analytical equipment is minor.

4.2 Site Parameters as Explaining Factors of Tree Nutrient Status

In our material P deficiencies occurred in every second experimental stand, and N and K deficiencies in every third or fourth analyzed needle sample. This result is in good agreement with previous studies carried out in Finland. A P shortage was reported in 30–70% of the nutrient-poor pine bogs in Central Ostrobothnia, while 15–30% suffered from a lack of K and 10–25% from a lack of N (Hytönen and Kokko 2006). Similar results have also been found in other studies (Moilanen 1992, Silver and Saarinen 2001).

The original (pre-drainage) mire site type proved to be an important factor explaining the nutrient status of Scots pine. This finding was the most important result in this study, and confirmed earlier suggestions concerning the connection between the mire origin and its nutrient status and development (e.g. Moilanen 1993, Silfverberg and Moilanen 2008). On forested sites, the nutrient status of the trees was in most cases adequate, whereas on sparsely forested and treeless sites, P and K deficiencies and shortages in relation to N were common. According to the present

study, the optimal growth habitats as regards the availability of the main nutrients (N, K, P) are originally forested sites classified as the dwarf-shrub forest site type after drainage (Vasander and Laine 2008).

The fertility level of a site (classified after drainage) was also found to determine the nutrient status of the trees. As was to be expected, the more fertile the site, the higher was the foliar N concentration. The situation with respect to the P and K concentrations was the opposite – P and K deficiencies and unbalanced nutrient ratios became more pronounced as the site fertility increased. This finding agrees well with the results of previous studies, which suggested that nutrient problems – especially for K – are the most common on N rich sites (Kaunisto and Tukeva 1984, Moilanen 1993).

The foliar K concentration decreased with increasing peat thickness. On thick-peated sites, K deficiencies can be explained by the low amount and availability of K in relation to N (Kaunisto and Paavilainen 1988, Kaunisto and Moilanen 1998). The present study confirms the result obtained by Saarinen (1997), according to which peat thickness (for over 40–50 cm layers) and the original pre-drainage site type (fen or bog) can be used to identify sites where K deficiencies are likely to occur. Foliar N was not dependent on the peat thickness on forested and treeless sites, but it was on sparsely forested sites: the N concentration increased slightly with increasing peat depth. This might be a consequence of the differences in fertility and peat types, and also in the degree of humification between the deep-peated original site types.

Variation in the annual weather conditions was reflected in the nutrient status of the current needles. The foliar N concentration increased with increasing temperature sum of the growing season. This result is interesting as regards growth capability and productivity, because sufficient N availability is a prerequisite for high wood productivity. Insufficient N mineralization and problems in N uptake have been noted in cool conditions (< 950 d.d.) (Starr and Westman 1978, Westman 1979, Sundström et al. 2000, Pietiläinen and Kaunisto 2003). In this study, the foliar N concentration on ‘N-poor’ dwarf-shrub/cottongrass sites was generally at the deficiency

level when the temperature sum was less than 950 d.d. In contrast, foliar N concentration on 'N-rich' tall-sedge and herb-rich sites was in most cases above the deficiency limit even during the coldest growth seasons.

The geographical variation in the nutrient status of trees is caused by climatic and weather conditions, as well as to the site's geological history leading all the way back to the melting period at the end of the last glacial age. In the present study, on the average the K concentration was the higher, the further away from the coast and the higher above from the sea level the stand was. This was especially apparent in younger drainage areas and in stands with low foliar N concentrations. This partially confirms the hypothesis regarding the effect of a receding sea line on the properties of mires forming in its wake, and on the nutritional status of the trees that grow there (Laiho et al. 2008). The hypothesis is that the ancient sea waters, while receding, leached out mineral nutrients from the area, resulting in a higher susceptibility to K deficiency. In this study, the foliar K concentrations were low especially on nitrogen-rich sites when the altitude of the site was less than 100 m a.s.l. and the location less than 100 km from the coast. However, the K status was in most cases adequate further away the sea when the altitude of the site exceeded 150 m a.s.l. This elevation approximately corresponds to the shoreline of the post-glacial Ancylus lake.

The growth and vitality of a tree stand is governed not only by individual nutrients, but also by their ratios in relation to one another inside the tree. A stand might be in a balanced nutrient status, even though it receives only small amounts of individual nutrients. On the other hand, a severe deficiency of a single nutrient can stunt growth seriously and cause a nutrient imbalance, even when the other nutrients are readily available. The optimal N:P ratio for needles is considered to be 11, and the optimal N:K ratio 3–3.5 (e.g. Puustjärvi 1962a, 1962b). In this study, the most imbalanced nutrient status – surplus N compared to K – was found in stands growing on thick-peated, originally treeless mesotrophic fens. The most balanced nutrient (N P K) status was in stands growing on originally thin-peated forested sites.

4.3 Development in Stand Nutrient Status over a Longer Period

As a result of drainage, the surface peat undergoes changes that may have an effect on the stand's nutrient status over a long period of time. The amount of N in the surface peat has been found to increase in the rooting zone (Kaunisto and Paavilainen 1988, Moilanen et al. 1996) as the water table level falls, the surface peat becomes compressed and the decomposition rate increases as a result of enhanced microbial activity. The amount of N available has also been assumed to increase with increasing drainage age as the deeper, N rich peat layers eventually come within reach of the root systems. In this study, however, elevated foliar N levels were not detected even on the oldest (50–75 years) drainage areas.

A 10% increase in the effective temperature sum resulted in an almost equal relative increase in needle N concentrations, and a corresponding decrease in needle K concentrations. Thus, the imbalance in the nutrient ratio appears to intensify following warm growing seasons. Accelerating N mobilization will most likely result in fewer cases of N deficiencies, but will pronounce the imbalance between N and other mineral nutrients.

There are some discrepancies in our current knowledge concerning the long-term requirements of K on thick-peated mires. On originally forested and unthinned mires, the amount of K in the peat does not usually decrease after drainage (Laiho and Laine 1995). However, especially on old drainage areas on fens that have undergone felling, the peat K concentrations have been as low as one half of those in a pristine mire of the corresponding site type (Kaunisto and Paavilainen 1988). It is still uncertain to what extent the contradictory results between various studies can be explained by nutrient losses in connection with the removal of logging residues, or by increased K leaching after logging.

This study included both young and old drainage areas, which made it possible to examine the post-drainage nutrient status of Scots pine over longer periods. Changes in nutrient concentrations relating to drainage age were relative minor. However, the needle K concentration was lower on the oldest sites compared to the younger sites – especially when the temperature sum was < 1000

d.d.. The phenomenon was most clearly visible on stands with high foliar N concentrations and on mires which, in their pristine stage, had been sparsely forested or treeless. The result is logical, because it is exactly on those site types that the total K pool in the peat is small. No noticeable deterioration in the K status was, however, found over the examined period (80 years from drainage).

Effect of drainage age on P was somewhat the opposite: there was an increasing trend in foliar P concentrations on thin-peated originally forested sites under higher temperature sum conditions. This could be due to the accelerated P mineralization in warmer weather conditions, and to the fact that the roots of the trees will eventually reach the underlying mineral soil, which is an additional source of P.

5 Conclusions

When estimating the nutrient status and fertilization requirements in peatland forestry, it is important to know the original nature of the drained area: whether it was a forested site type or a treeless fen. This should be taken into account when developing fertilization recommendations for peatland forests.

In order to avoid growth losses and to improve the nutrient status, fertilization should be directed towards the 'N-rich' site types, which are deep-peated, and the stands are suffering from an unbalanced availability of N versus P and K. Furthermore, as a lack of K in peatland stands usually coincides with a lack of P, it is advisable to apply both K and P in a single treatment.

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