# Changes in plant cover of a mire in southern Karelia, Russia over 50 years following drainage

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## SUMMARY

Long-term monitoring of middle taiga wetland vegetation has been undertaken at the Kindasovo Forest and Mire Research Station, which is located within the Koivu-Lambasuo Nature Reserve in southern Karelia (north-west Russia). This article revisits the results of 50 years' monitoring of post-drainage succession in a meso-oligotrophic dwarf shrub - *Sphagnum* pine mire. The purpose of drainage was to improve the quality of the site for forestry. Gradient analysis and Ellenberg's indicator values were used to associate differentiation of the plant cover with the main environmental factors (availability of moisture and light, soil acidity, soil mineral nitrogen content), and thus to distinguish three chronological drainage periods on the basis of changes in the plant communities, which are then described. The initially understocked dwarf shrub - *Sphagnum* pine stand (low quality forest) evolved over 50 years into a well-stocked pine stand, but this was not a sufficient period for the ground cover vegetation to reach a new stable state. Nonetheless, analysis of species composition dynamics during the three drainage periods showed that species diversity increased from 17 to 31 species, wetland species were preserved but their prevalence and percentage cover declined, and forest-associated species appeared.

**KEY WORDS:** Ellenberg's indicator values, forestry, gradient analysis, peatland, vegetation dynamics

## INTRODUCTION

Human pressure can be detrimental for natural wetland ecosystems such as paludal forests and mires. On the other hand, the outcome of an intervention can be positive if a knowledge-based forecast of the resulting transformation is available. In other words, understanding how these ecosystems function and interact with environmental factors can help us to avoid negative effects. This, in turn, requires a thorough study of vegetation and plant community productivity in different mire types during natural and human-induced successions.

In the Republic of Karelia (north-west Russia), boreal mires occupy 3.63 million hectares (21 % of the land area) and paludified forests 1.83 million ha (10.6 %) (Piavchenko & Kolomytsev 1980). The spatial extent of forested mires is not great, and almost half of them carry understocked and low-productivity pine stands. Tree and tree - *Sphagnum* plant communities occur far more frequently within other mire types, especially in their margins. Here, the issue of extensive paludal land cover was addressed in the mid-20th-century by drainage, which has altered natural landscapes substantially. The resulting changes in mire and paludal forest vegetation have been studied quite extensively in both Finland and Russia. For example, Sarasto (1957) studied post-drainage successions in Finland; while Neshataev (1986) studied the successions initiated by drainage of herb-*Sphagnum* pine forests in the Leningrad Region of Russia, and in a monograph compiled by Fedorchuk *et al.* (2005) provided information about ecosystem variation in the major forest types, including changes in plant communities during age-related and regenerative successions of tree stand composition in drained areas

In general, research has focused primarily on the effects of drainage on the tree layer. At the Russian Academy of Sciences (RAS) West Dvina Research Station in Tver Oblast, bog forest ecosystems are studied in the context of experimental forest drainage (BIMFC 1982); and for West Siberia, Efremov (1987) has summarised the results of 20 years of station-based research which focused on integrated assessment of the process of pioneer tree stand formation in treeless and sparsely wooded drained mires. In Karelia, natural forest regeneration in the first 10–15 years after drainage were studied by Medvedeva & Matyushkin (1981) and by Sakovets *et al*. (2000).

Much less frequent are recurrent surveys of permanent sample plots during the first decades following drainage which aim to provide insights into the mechanisms by which drainage affects not only the vegetation, but also the soil and the environmental conditions. The latter approach was adopted at the Kindasovo Forest and Mire Research Station of the RAS Karelian Research Centre, where multidisciplinary research into the structure and dynamics of natural and drained mires and paludified forests began in 1969 under the leadership of Corresponding Academician N. P'yavchenko. The research was carried out in two stages, the first stage focusing on the vegetation of natural (non-drained) mires and the second on dynamics of the cover, structure and productivity of plants in the mire complexes starting from the first decade following the commencement of drainage.

The aim of this article is to assemble and describe the results of 50 years of research at Kindasovo concerning the post-drainage dynamics of species composition and structure of the plant cover, and to gain insights about which environmental factors influenced the development of mire vegetation after drainage. The specific objectives are to examine plant diversity in a drained meso-oligotrophic dwarf shrub - *Sphagnum* pine stand, and to carry out retrospective gradient analysis to investigate how the principal environmental factors have influenced its differentiation.

## METHODS

### Study area and research context

The Kindasovo Forest and Mire Research Station is situated in middle taiga within the Koivu-Lambasuo Nature Reserve in southern Karelia (north-west Russia). Long-term average climate characteristics are as follows: duration of the growing season is 148 days, air temperature during the growing season is 11.7 °C, and annual precipitation is 565 mm of which 316 mm falls during the growing season (Chesnokov 1979). The main south-Karelian mire types are: *Sphagnum* ridge-hollow oligotrophic; herb - *Sphagnum* mesotrophic; herb - *Sphagnum* - *Hypnum* (Karelian concentric aapa); and *Sphagnum* pine mesotrophic (Elina *et al*. 1984), all of which are represented within the Nature Reserve. Most of the mires remained in natural (virgin) state until parts of them were drained in 1969–1974.

The first stage of research (from 1969) began with an analysis of aerial photographs to determine the proportions of different vegetation complexes in the mires (Galkina 1969). Within the mire complexes identified from the aerial images, the most typical sites (in terms of microtopography and plant cover) were selected as representative sample plots (SPs) to be monitored on a permanent basis. All in all, eleven SPs of size 0.3–0.5 ha were established. Prior to drainage, geobotanic relevés were made, peat was sampled and analysed for botanical composition and stage of decomposition, and water table depth (WTD) was measured in hollows, lawns, hummocks and ridges within each SP. The spatial structure of the plant cover was studied by large-scale mapping of a single permanent sampling plot (PSP) per SP, whose dimensions (50–150 $m^2$) depended on the structural complexity of the mire and the sizes of individual microtopographical features. Also within each SP, 20–25 permanent (1 × 1 m) monitoring plots (PMPs) were established.

In the second stage of research (after drainage), the previous studies were elaborated in more detail. Changes in species composition and structure of the plant cover were studied by established and modified methods (Grabovik 1989, Grabovik *et al*. 2019). However, the focus was on the structure and dynamics of the plant cover, meaning that the measurement of WTD (and other environmental factors) throughout each growing season was not included in the tasks of this investigation.

### Study site and field measurements

For the present study, we selected a single mire SP of size 0.3 ha (Figure 1), situated at the foot of an eroded esker ridge and classified as a dwarf shrub - *Sphagnum* pine stand at co-ordinates 61° 43' 58.9" N, 33° 27' 0.4" E. When the geobotanic relevé was recorded, the flora comprised 20 species: two trees, six dwarf shrubs, three herbs, and nine mosses. In 1970, the mire was drained by installing a network of open drains (ditches) spaced 160 m apart, which have subsequently become overgrown by herbaceous vegetation.

In the selected site the size of the PSP was 100 $m^2$ (10 × 10 m) and it was situated in the central part of the SP (Figure 1). Large-scale mapping of the PSP was carried out in the year of drainage and repeated 25 and 50 years later, in 1995 and 2020. WTD was measured in hummocks and lawns of the PSP at the same times. Sampling of peat for botanical analysis was repeated once, in 2003.

Changes in the plant cover of field and ground layers were monitored in 20 PMPs (1 × 1 m) established on lawns and hummocks scattered across an 80 m wide strip along a ditch within the SP (Figure 1). The first (control) observations (% cover of plant species) were recorded in the year the peatland was drained (1970). These observations were subsequently repeated at intervals of 1–3 years until 1978, then at intervals of 1–4 years from 1989


Figure 1. Aerial view of the study site (meso-oligotrophic dwarf shrub-*Sphagnum* pine stand). 1: sample plot (SP; 0.5 ha); 2: permanent sample plot (PSP; 100 m$^2$); 3: permanent monitoring plots (PMPs; 1 m$^2$); 4: melioration channels.

until the present. In the results reported here, the taxonomy of vascular plants follows Cherepanov (1995) with adjustments based on a later publication by Kravchenko (2007); and moss taxonomy follows Ignatov *et al*. (2006).

Tree layer growth in a 40-m-wide strip along the ditch was assessed in the year of drainage, and then 25 and 50 years after drainage. The main tree stand quality characteristics were determined according to the Russian forest appraisal system (Anuchin 1982). In this system, site quality (bonitet) indicates potential stand productivity, which depends on habitat conditions and tree growth rates, and is determined from the mean age and mean height of the stand. Greater height and timber value of the stand at a given age corresponds to higher site quality. Stands assigned to Site Classes I–II are described as high-productivity (high quality), those in Classes III-IV are medium-productivity (medium quality), and those in Classes V, Va and Vb are unproductive (low quality).

**Aids to interpretation of data**

Plants are nowadays used as indicators of various environmental and ecological factors. Indicators can be individual species, ecological and coenotic groups, or plant communities and their floristic composition. To support the interpretation of vegetation changes observed in this study we used two indicator systems based on the presence of individual species in the field and ground layers.

Ellenberg's indicator values are presented as a table where the reactions of individual species to environmental factors are given as scores representing the positions of the species' synecological optima on a gradient of the factor (Ellenberg *et al*. 1991). Ellenberg suggested value scales (based on the presence/absence of particular species) for: light–shade, soil moisture, soil reaction, mineral nitrogen content in soil, temperature and continentality. From the PMP species lists recorded for each year of the study, we derived Ellenberg's indicator values for:

- light (scores ranging from 1 for full-shade plants, which usually receive < 1 % of full light; to 9 for full-light plants, which usually receive more than 50 % of full light);
- soil moisture i.e. preferences for soil moisture or water table depth (scores ranging from 1 for species growing on very dry soils; to 12 for submerged plants that are periodically or constantly underwater);
- soil acidity i.e. soil or water pH (scores ranging from 1 for species growing only on very acidic

soils; to 9 for those growing only on alkaline and Ca-rich soils); and

- soil mineral nitrogen content (scores ranging from 1 for species growing on soils that are very poor in mineral nitrogen; to 9 for those growing on soils very rich in nitrogen).

The species recorded in the PMPs were also assigned to the eco-coenotic groups (ECGs) of Kuznetsov (2005), which are constant for Karelia and are used to identify and characterise plant communities according to their relationships with habitat conditions. These groups comprise vascular plants of different life forms (excluding woody species, which have broad ecological amplitudes), mosses and lichens. They were distinguished empirically for Karelian mires on the basis of habitat preferences of different species regarding moisture, flow rate, light conditions and trophic status, as well as continuity in the communities (Kuznetsov 2002). Kuznetsov (2005) distinguished 12 ECGs, of which five (1–3, 5 and 12) are represented in meso-oligotrophic dwarf shrub-*Sphagnum* pine stands. ECG 1 is typical for meso-oligotrophic pine bog on shallow peat situated in the mire margin. Species placed in ECG 2 usually occupy hummocks with slow peat deposition, whereas those in ECG 3 all have a broad ecological amplitude and are abundant on lawns, their dominance being a good indicator for differentiating lawns. ECG 5 is also typically found on lawns in meso-oligotrophic sites. ECG 12 includes a range of species characteristic of forests of different types, and occurs mainly in treed communities on mires, most often on tree-base hummocks. The presence of forest species is an indicator of variable moisture conditions and a dynamic interplay between mire and forest.

### Gradient analysis

In order to gain insights about the key environmental factors for plant cover differentiation, the ecological features of the plant communities observed in the PMPs at the different survey dates, along with their positions in environmental space, were determined using gradient analysis performed by the non-metric multidimensional scaling (NMS) method (Kruskal & Wish 1978) in the geobotanic data processing application PC-ORD 6.12. The variable analysed was the percentage cover of species recorded in the PMPs over the years of study since 1969. In the absence of direct measurements of environmental factors, ordination gradients were interpreted using the Ellenberg indicator values derived from the same vegetation data (see above). Ordination axis loads were calculated using Sørensen's index, after-the-fact by comparing the variance captured in an axis with the total variance in the empirical data table (McCune & Mefford 2011). Correlations were established between the ordination axes and the environmental factors.

## RESULTS

### Environmental factors and gradient analysis

Vectors of the four Ellenberg indicator values derived from the gradient analysis, for each year when PMP data were recorded, are shown in Table 1. From 1970 to 2020 there were declining trends for the light (from 7.4 to 5.9) and soil moisture (from 8.5 to 6.8) factors, and slight increases for the trophic factors soil acidity (from 2.3 to 2.6) and mineral nitrogen content in soil (from 1.8 to 2.4). The trends are shown more clearly by the NMS ordination plot for the 50 years spanned by the study (Figure 2). The first axis is the principal gradient and explains 85.9 % of the total variance, while the second axis explains 8.4 % of total variance. The ordination plot exhibits a clear chronological gradient from 1970 to 2020, and all four environmental factors have high levels of correlation with the first axis: light (r = -0.878), soil moisture (r = -0.524), soil acidity (r = 0.514), and mineral nitrogen content in soil (r = 0.782). We distinguished three groups (assemblages) of plant communities along the chronological gradient, each with its own specific moisture, light, and nutrient levels. The groups are quite distinct in the NMS ordination space, with hardly any overlaps. On this basis we associated the plant assemblages recorded with three distinct 'drainage periods': (I: 1970–1978; II: 1989–2000; and III: 2001–2020). The gap between Groups I and II is probably due to the long gap in data input from 1978 to 1989 (Table 1). The drainage periods are used below as the basis for description of the sequence of changes that occurred in the SP over the 50 years following drainage.

### Changes in site condition through time

*Prior to drainage (1969–1970)*

Before the site was drained, the mire surface had pronounced microtopography with hummocks distributed across an undulating lawn. On hummocks, the ground layer was formed by *Sphagnum angustifolium* and the field layer was dominated by *Chamaedaphne calyculata* and *Carex globularis*. On lawns, the ground cover was provided by *Sphagnum angustifolium* with some *Sphagnum divinum* and the field layer dominants were the dwarf shrubs *Andromeda polifolia* and *Oxycoccus palustris* along with the sedges *Carex globularis* and *Carex lasiocarpa*. The percentage cover of mosses was

Table 1. The basic environmental factors for vegetation communities of meso-oligotrophic dwarf shrub-*Sphagnum* pine stand resulting from the 50 years research (Ellenberg's indicator values). The dotted lines indicate the transitions between Drainage Periods (Figure 2).

| Years of investigation | Vectors of environmental variables | | | |
|---|---|---|---|---|
| | Light | Soil moisture | Soil acidity | Mineral nitrogen content in soil |
| 1970 | 7.4 | 8.5 | 2.3 | 1.8 |
| 1972 | 7.5 | 8.5 | 2.3 | 1.9 |
| 1973 | 7.3 | 8.4 | 2.2 | 1.8 |
| 1975 | 6.3 | 5.7 | 1.6 | 1.7 |
| 1978 | 7.4 | 8.3 | 2.3 | 2.0 |
| 1989 | 6.9 | 7.8 | 2.2 | 1.7 |
| 1990 | 6.5 | 7.6 | 1.7 | 1.8 |
| 1992 | 6.5 | 7.6 | 2 | 1.8 |
| 1996 | 6.3 | 6.9 | 2.1 | 2.1 |
| 1997 | 6.5 | 7.4 | 1.9 | 2.0 |
| 1998 | 6.4 | 7.2 | 2.3 | 2.0 |
| 1999 | 6.4 | 7.4 | 2.4 | 2.0 |
| 2000 | 6.3 | 7.3 | 2.5 | 2.0 |
| 2001 | 6.3 | 7.5 | 2.5 | 2.1 |
| 2002 | 6.3 | 7.5 | 2.5 | 2.3 |
| 2004 | 6.2 | 7.1 | 2.5 | 2.3 |
| 2007 | 6.1 | 6.9 | 2.5 | 2.3 |
| 2009 | 6.2 | 7.1 | 2.5 | 2.1 |
| 2020 | 5.9 | 6.8 | 2.6 | 2.4 |

ubiquitously 100 %, while the field layer cover was 70 % on hummocks and 60 % on lawns. The horizontal structure of the plant cover revealed by analysis of the PSP map and relevé data indicated that the site was predominantly (76 %) occupied by lawn communities of *Chamaedaphne calyculata* - *Carex lasiocarpa* - *Sphagnum angustifolium*, whereas the plant cover on hummocks (24 %) was provided by communities of *Chamaedaphne calyculata* - *Carex globularis* - *Sphagnum angustifolium* + *Polytrichum strictum*, and *Chamaedaphne calyculata* - *Oxycoccus palustris* - *Sphagnum divinum*.

At this time, WTD was 15 cm in lawns and 30 cm in hummocks. The soil was described as peaty gley with a layer of transitional peat 30–50 cm thick overlying clay. The upper horizon (0–16 cm) was made up of little decomposed (5 %)[1] *Sphagnum* peat with low ash content (3.0–4.7 %) and main constituents *Sphagnum angustifolium*, *Sphagnum capillifolium* and *Sphagnum* species belonging to Section Cuspidata. The lower (16–30 cm) sedge-*Sphagnum* peat was composed of remains of *Carex lasiocarpa*, *Carex rostrata* and *Carex globularis*, together with *Sphagnum angustifolium*, *Sphagnum capillifolium* and *Sphagna* belonging to Section Cuspidata. This deeper horizon had medium levels of decomposition (25 %) and ash content (19 %), and was acidic with low base saturation (23–40 %), Total nitrogen content in both horizons was 0.8–1.0 % (CSMWK 1976).

The tree layer consisted of pine and birch trees 1–2 m tall belonging to Site Class Va (low quality), and the stand was classified as understocked with a relative stocking rate of 0.3. The densities of regenerating pine and birch were 300 and 780 saplings ha$^{-1}$, respectively.

[1] Degree of biochemical decay, determined by the 'USSR centrifugation method' described by Malterer *et al*. (1992), as originally devised by Lishtvan & Korol' (1975).

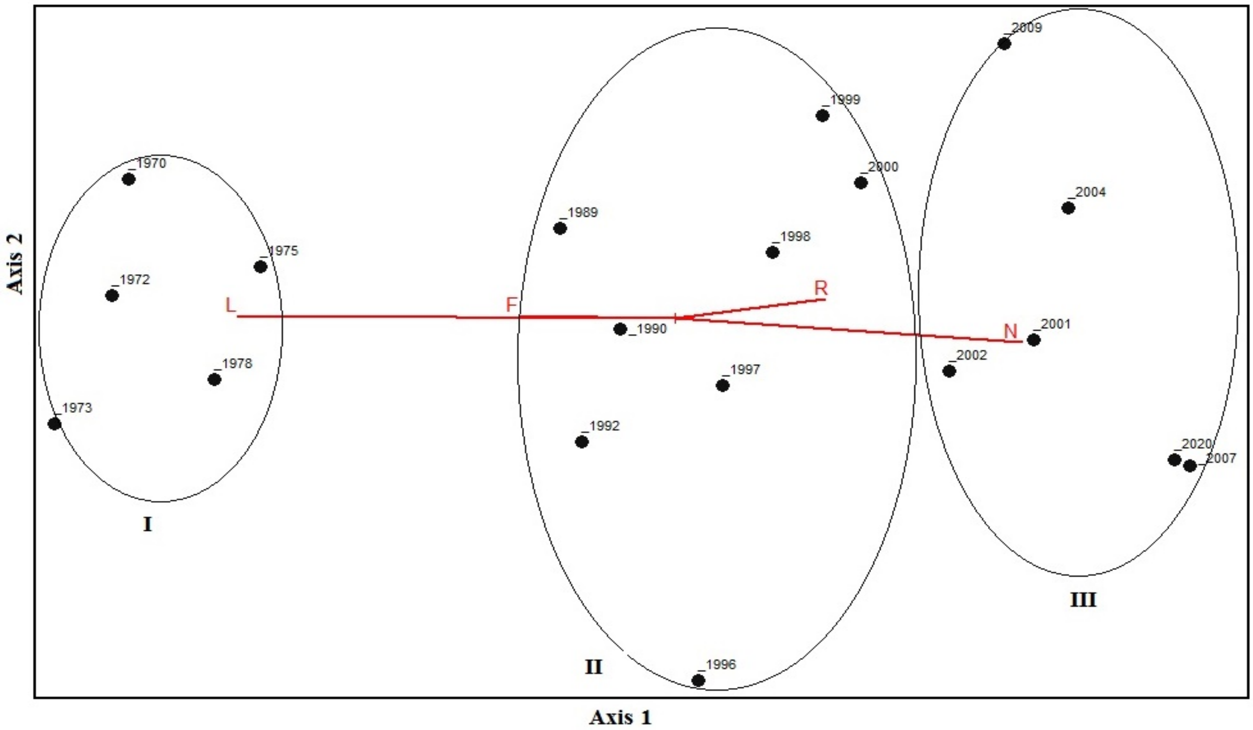


Figure 2. NMS ordination plot for the distribution of relevés over the 50 years of studies (from 1970 to 2020). Roman numerals indicate the ‘drainage periods’ (I: 1970–1978; II: 1989–2000; III: 2001–2020. Vectors of environmental variables are shown in red and labelled L: light; F: soil moisture; R: soil acidity; N: mineral nitrogen content in soil.

*Drainage Period I (1970–1978)*

During this period, the dominant species recorded in the PMPs were *Andromeda polifolia, Chamaedaphne calyculata*, *Carex globularis*, *Carex lasiocarpa*, *Oxycoccus palustris*, *Vaccinium uliginosum*, *Sphagnum angustifolium* and *Sphagnum divinum.* These species belong to ECGs 1, 3, and 5 (Table 2), which have wide ecological amplitudes and are characteristic of the oligotrophic sparse pine bog communities growing in mire margins with shallow peat deposits (Kuznetsov 2005). The indicator species for this period were *Chamaedaphne calyculata*, *Carex globularis*, *Sphagnum angustifolium* and *Sphagnum divinum*, which retained their high constancy and percentage cover except that the percentage cover of *Carex globularis* declined from 24 % to 13 %. The species composition and structure of the field (dwarf shrubs and herbs) and ground (mosses) layers in typical lawn and hummock communities remained similar to the original state, with the same dominant species as prior to drainage.

*Drainage Period II (1989–2000)*

The PMP data collected during the second drainage period show that *Sphagnum* mosses remained dominant in the ground layer (percentage cover > 50 %; Table 2) and peat formation was still in progress, although the moss carpet was loose. The field layer on lawns retained a majority of mire species (ECGs 1, 2, 3), but their vitality had declined and they did not flower or bear fruit. Although the occurrence of these species had not changed, their percentage cover had dropped to half or one-third of original values. The cover of herbs had become sparser and *Carex lasiocarpa* had disappeared. Moreover, forest species belonging to ECG 12 had appeared in minor amounts. These species included *Calamagrostis neglecta*, *Equisetum sylvaticum*, *Melampyrum sylvaticum* and *Vaccinium myrtillus*, along with the typical dry-forest inhabitants *Brachythecim reflexum*, *Dicranum scoparium* and *Pohlia nutans* which colonised the lower parts of tree-bases. Large-scale re-mapping of the PSP (in 1995) showed that lawns now occupied 88 % and hummocks 12 % of total area, and tree - *Sphagnum* plant communities prevailed. WTD was 25 cm in lawns and 40 cm in hummocks.

By 1995 the forestry stocking index had increased to 0.8 and the tree stand was in Site Class III (medium quality). The tree stand formula was $7P_{45}3B_{40}$ (70 % 45-year-old pine and 30 % 40-year-old birch), the

Table 2. Post-drainage changes in species composition of the plant cover at the study site. Numbered plant species correspond to eco-coenotic groups (ECGs). Constancy classes are represented by Roman numerals with mean projective cover (%) as a superscript. Data are shown for representative (not all) years of the study.

| Plant species | Drainage periods / Years | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | I | | | | | II | | | | III | | | | | | |
| | 1970 | 1972 | 1973 | 1975 | 1978 | 1989 | 1992 | 1996 | 1998 | 2000 | 2001 | 2002 | 2004 | 2007 | 2009 | 2020 |
| *1.Carex globularis* | IV$^{24}$ | V$^{19}$ | V$^{12}$ | V$^{13}$ | V$^{13}$ | V$^{10}$ | V$^{8}$ | V$^{6}$ | V$^{6}$ | V$^{6}$ | V$^{7}$ | V$^{6}$ | V$^{5}$ | V$^{7}$ | V$^{8}$ | V$^{6}$ |
| *Vaccinium uliginosum* | III$^{6}$ | IV$^{8}$ | V$^{10}$ | V$^{14}$ | V$^{14}$ | V$^{21}$ | V$^{21}$ | V$^{24}$ | IV$^{18}$ | IV$^{11}$ | IV$^{12}$ | V$^{15}$ | IV$^{7}$ | IV$^{5}$ | IV$^{5}$ | IV$^{5}$ |
| *Sphagnum capillifolium* | III$^{7}$ | I$^{8}$ | V$^{28}$ | II$^{6}$ | III$^{8}$ | – | III$^{11}$ | III$^{13}$ | II$^{7}$ | I$^{+}$ | – | – | – | – | – | – |
| *2.Sphagnum fuscum* | – | – | – | – | I$^{2}$ | I$^{+}$ | I$^{+}$ | – | II$^{3}$ | I$^{4}$ | – | – | I$^{1}$ | – | – | – |
| *Polytrichum strictum* | – | II$^{5}$ | III$^{7}$ | – | I$^{2}$ | – | I$^{3}$ | I$^{2}$ | I$^{1}$ | I$^{1}$ | II$^{2}$ | II$^{2}$ | – | I$^{1}$ | – | I$^{1}$ |
| *Cladina sylvatica* | I$^{1}$ | I$^{1}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | – | I$^{+}$ | – | – | – | – |
| *3.Andromeda polifolia* | IV$^{5}$ | V$^{4}$ | V$^{6}$ | V$^{6}$ | V$^{7}$ | IV$^{3}$ | III$^{2}$ | II$^{1}$ | III$^{1}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ |
| *Chamaedaphne calyculata* | V$^{17}$ | V$^{16}$ | V$^{15}$ | V$^{12}$ | V$^{16}$ | V$^{11}$ | V$^{14}$ | V$^{7}$ | V$^{5}$ | V$^{6}$ | IV$^{5}$ | IV$^{5}$ | IV$^{3}$ | III$^{4}$ | IV$^{4}$ | III$^{4}$ |
| *Eriophorum vaginatum* | III$^{4}$ | I$^{+}$ | V$^{11}$ | I$^{+}$ | – | I$^{+}$ | III$^{1}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | – | I$^{+}$ | III$^{1}$ | I$^{+}$ |
| *Oxycoccus palustris* | V$^{11}$ | V$^{9}$ | V$^{12}$ | V$^{12}$ | V$^{10}$ | V$^{9}$ | V$^{10}$ | – | IV$^{3}$ | IV$^{3}$ | V$^{3}$ | V$^{4}$ | IV$^{2}$ | III$^{1}$ | IV$^{1}$ | III$^{1}$ |
| *Sphagnum angustifolium* | V$^{50}$ | V$^{44}$ | V$^{55}$ | V$^{44}$ | V$^{43}$ | V$^{54}$ | V$^{53}$ | V$^{54}$ | V$^{33}$ | V$^{22}$ | V$^{33}$ | V$^{37}$ | V$^{16}$ | V$^{28}$ | V$^{23}$ | V$^{28}$ |
| *Sphagnum divinum* | V$^{34}$ | V$^{27}$ | V$^{42}$ | V$^{31}$ | V$^{28}$ | V$^{19}$ | V$^{14}$ | V$^{18}$ | V$^{17}$ | V$^{22}$ | V$^{26}$ | V$^{24}$ | V$^{15}$ | V$^{20}$ | V$^{23}$ | V$^{20}$ |
| *5.Carex lasiocarpa* | IV$^{6}$ | V$^{4}$ | V$^{7}$ | IV$^{4}$ | V$^{7}$ | I$^{+}$ | – | – | – | – | – | – | – | – | – | – |
| *12.Calamagrostis neglecta* | – | – | – | – | – | – | I$^{+}$ | – | – | – | I$^{+}$ | I$^{+}$ | I$^{+}$ | – | – | – |
| *Goodyera repens* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | I$^{+}$ |
| *Equisetum sylvaticum* | – | – | – | – | – | – | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | II$^{1}$ | II$^{+}$ | II$^{+}$ | II$^{+}$ | I$^{+}$ | II$^{+}$ |
| *Melampyrum sylvaticum* | – | – | – | – | – | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ |
| *Luzula pilosa* | – | – | – | – | – | – | – | – | – | – | – | – | – | – | I$^{+}$ | I$^{+}$ |
| *Vaccinium myrtillus* | – | – | – | – | – | I$^{+}$ | I$^{+}$ | – | I$^{+}$ | – | II$^{5}$ | I$^{+}$ | I$^{+}$ | II$^{1}$ | I$^{1}$ | II$^{1}$ |
| *Vaccinium vitis-idaea* | I$^{+}$ | I$^{1}$ | II$^{+}$ | II$^{1}$ | III$^{2}$ | III$^{3}$ | IV$^{8}$ | IV$^{11}$ | V$^{10}$ | IV$^{9}$ | IV$^{10}$ | III$^{10}$ | III$^{9}$ | III$^{8}$ | IV$^{11}$ | III$^{8}$ |
| *Lycopodium clavatum* | – | – | – | – | – | – | – | – | – | – | – | – | – | I$^{+}$ | I$^{1}$ | I$^{+}$ |
| *Aulacomnium palustre* | I$^{+}$ | – | – | II$^{+}$ | II$^{+}$ | II$^{+}$ | I$^{+}$ | II$^{+}$ | I$^{+}$ | II$^{+}$ | II$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | – | I$^{+}$ |
| *Brachythecim reflexum* | – | – | – | – | – | – | – | – | I$^{+}$ | I$^{+}$ | – | – | – | – | – | – |
| *Dicranum scoparium* | – | – | – | – | – | – | – | – | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | – | – | I$^{+}$ | – |
| *Pleurozium schreberi* | I$^{4}$ | I$^{4}$ | II$^{6}$ | II$^{7}$ | II$^{5}$ | II$^{7}$ | II$^{8}$ | II$^{7}$ | II$^{6}$ | III$^{8}$ | III$^{8}$ | III$^{8}$ | II$^{5}$ | III$^{6}$ | III$^{10}$ | III$^{6}$ |
| *Pohlia nutans* | – | – | – | – | – | – | I$^{+}$ | – | I$^{+}$ | – | – | – | – | – | I$^{+}$ | – |
| *Polytrichum commune* | II$^{7}$ | II$^{7}$ | I$^{1}$ | II$^{7}$ | II$^{6}$ | II$^{4}$ | I$^{+}$ | I$^{+}$ | II$^{1}$ | II$^{2}$ | I$^{+}$ | I$^{+}$ | II$^{2}$ | I$^{+}$ | II$^{2}$ | I$^{+}$ |
| *Ptilium crista-castrensis* | – | – | – | – | – | – | – | – | – | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | I$^{+}$ | – | I$^{+}$ |
| *Sphagnum russowii* | – | – | – | – | – | III$^{7}$ | – | – | III$^{7}$ | IV$^{13}$ | II$^{3}$ | II$^{4}$ | III$^{8}$ | I$^{1}$ | – | I$^{1}$ |

standing stock was 100 $m^3$ $ha^{-1}$, and the proportion of birch had increased. For the pine trees, average diameter was 12.7 cm, average height was 11 m, and there were no coniferous seedlings or young regrowth.

*Drainage Period III (2001–2020)*

The PMP data collected during this drainage period showed that the prevalence of mire plants in lawns declined insignificantly, although their percentage cover halved and colonisation by the forest species *Lycopodium clavatum*, *Goodyera repens* and *Ptilium crista-castrensis* occurred. The ECG affiliations of the forest species indicate variable moisture and air conditions, along with dynamic interactions between mire and forest. Large-scale re-mapping of the PSP (in 2020) showed that lawns occupied 8 % and hummocks 92 % of total area, and tree - *Sphagnum* plant communities still prevailed. WTD was 40 cm in lawns and 50 cm in hummocks.

The botanical analysis of peat was repeated in 2003 (after 33 years). The top layer (0–19 cm) was transitional *Sphagnum* peat in the initial phase of decomposition (5 %) (i.e. it was still peat-forming) and it was composed of the remains of *Sphagnum angustifolium*, *Sphagnum russowii* and *Sphagnum divinum* plus *Eriophorum, Carex globularis* and mire dwarf shrubs. The bottom layer (19–33 cm) was (apparently unchanged) medium-decomposed (25 %) sedge-*Sphagnum* peat made up of residues of *Carex lasiocarpa*, *Carex rostrata* and *Carex globularis* mixed with *Sphagnum angustifolium*, *Sphagnum divinum*, and *Sphagnum russowii*.

In 2020 the forestry stocking index was still 0.8 but the average diameter and height of trees in the dwarf shrub-*Sphagnum* pine forest had increased to 20.8 cm and 20.2 m, respectively. The pine stands were well-stocked examples of Site Class II (high-productivity) with total standing stock 230 $m^3$ $ha^{-1}$. The contribution of pine to the tree layer had increased, giving a tree stand formula of $8P_{70}3B_{65}$ (80 % 70-year-old pine and 30 % 65-year-old birch).

## DISCUSSION

The lack of changes in the ground and field layer vegetation during the eight years following drainage (Drainage Period I) can be attributed to the low drainage intensity (160 m between ditches). By 1989 (Drainage Period II), however, it was evident that drainage had induced changes in the plant cover on both lawns and hummocks. We associate the absence of pine regeneration at this time to the well-developed field layer and the relatively thick *Sphagnum* cover. The emergence of saplings may have been hindered by desiccation of the loose layer of *Sphagnum* mosses (in drier growing seasons) or, otherwise, by damping-off of seedlings during wet seasons. We dismiss grazing as a significant factor in controlling regeneration because we observed no evidence of elk or any other large herbivore, such as droppings and/or damage to the tops and bark of trees, at the site.

Of the environmental factors considered, the main triggers for changes of species composition in the drained habitats are likely to be changes in moisture and trophic status, while in this ecosystem the light factor will depend on the trophic status and moisture availability. This is because the most striking response to drainage was observed in the tree layer, although effects may have been enhanced because we studied tree growth in the most intensely drained part of the mire. The forest quality characteristics recorded in 1995 and 2000 indicate that the site conditions had improved. As time passed following drainage, crown expansion increased the stand stocking rate and canopy closure which, in turn, changed the light conditions at the mire surface. The soil air and moisture conditions, along with trophic status, also improved, reducing the representation of mire species and augmenting the diversity of forest species.

Analysis of the literature shows that much of the available information regarding changes in the plant cover of mires and paludified forests is based on one-off surveys carried out quite a long time after drainage. Fedorchuk *et al.* (2005) demonstrated that the plant cover of peatlands in the north-west of European Russia returns to a state of relative stability no earlier than 20–25 years after perturbation by drainage. According to Finnish researchers (Heikurainen 1983, Laine 1989), the ground cover in drained peatlands establishes as a stable plant community different from the original type within 40 years after drainage. These authors also report that the formation of forests of various types after peatland and paludal forest drainage in Leningrad Region continued for 20–90 years. Finnish researchers (Laine *et al.* 1995) studied the ground cover vegetation in *Sphagnum* pine stands that had been drained 3–55 years previously. They observed that, in the first years after drainage, the hydrophilic sedges *Carex lasiocarpa* and *Carex rostrata* vanished. The percentage cover of wetland dwarf shrubs declined as the canopy moved towards closure, and as light availability declined the proportions of *Sphagnum* mosses were arranged in the following order: *Sphagnum fuscum* > *Sphagnum magellanicum* > *Sphagnum russowii*.

Hotonen *et al*. (1999) studied the effects of forest drainage on an aapa mire complex in the north boreal vegetation zone. Six mire site types were represented by 33 permanent sample plots whose plant cover was recorded around the time of drainage (in 1933) and thereafter in 1943, 1950 and 1994. The results showed that, in originally moist wooded bogs dominated by dwarf shrubs, the ground cover had been fully replaced by forest-dwelling species 60 years after drainage. Thus, when recording of the PSP and tree stand data for our site was repeated after 25 years (and certainly after 50 years), we might have expected that a sufficient period would have elapsed for the plant cover to acquire traits of stability and become relatively well-adapted to the post-drainage environmental conditions. In this dwarf shrub - *Sphagnum* pine stand, however, processes did not stabilise during the whole of our period of observations. Here, the ground cover on hummocks and lawns was dominated by mire dwarf shrubs, sedges and *Sphagnum* species prior to drainage, and even after 50 years the ground cover of lawns retained mire-associated species. However, the vitality of these species was declining, they neither flowered nor produced fruit, their prevalence and percentage cover had dropped by one-half or two-thirds, and forest species that were absent prior to drainage had appeared in minor amounts.

The changes and the succession of stages in the plant cover dynamics following drainage are characteristically diverse, depending both on drainage intensity and on the original type of the mire site. Drainage-induced changes in the plant cover of transitional mires in southern Karelia were studied after three years by T. Yurkovskaya. Her surveys showed not only that the species composition remained unchanged, but that even the quantitative ratios were nearly the same. Change was observed only in the roles of some sedge species in the communities. Comparative transect surveys of the plant cover of treeless herb - *Sphagnum* transitional bogs and *Sphagnum* pine stands that had been intensively drained 30–50 years previously demonstrated that the field-layer and ground-layer dominants in the resulting secondary forest communities were forest vascular plants and forest mosses. In cases of less intensive drainage, however, changes in the ground cover were minor; only the most hydrophilic mire plants disappeared, dwarf shrubs become more abundant, and forest plants appeared on elevated areas around tree trunks (Yurkovskaya 1963). Thus, it seems that changes in the ground cover depend on both the degree and on the duration of drainage.

The few available recurrent surveys of permanent sample plots covering the first decades after drainage provide better insights than one-off surveys into the mechanisms of drainage effects on all layers of the vegetation as well as on the soil and ecological conditions. Such studies were previously carried out at Kindasovo by Medvedeva (1989) and by Sakovets *et al.* (2005), who explored aspects of natural forest regeneration in the first 10–15 years after drainage. The study by Grabovik *et al*. (2019), also based on recurrent surveys, showed that the plant cover in the selected drained mesotrophic herb - *Sphagnum* mire had not attained stability 47 years after drainage, but that the succession process was directed towards a more mesophytic state of the plant communities compared to their original state.

The data reported here suggest that, where the drainage intensity is low, the ground cover cannot be used as an indicator of the effect on tree stand growth (Grabovik 1998). The significance of endogenous processes increases gradually over time after drainage and, in all likelihood, the change in ground cover depends much more on tree-layer canopy closure and root spread than on drainage intensity. Although the moss cover becomes loose, *Sphagnum* species retain dominance and peat formation continues. Drainage also causes the species diversity of the plant communities to increase, as species associated with boreal forest appear. In our case, drainage induced an increase in species diversity from 17 species in 1970 to 31 species in 2020.

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## AUTHOR CONTRIBUTIONS

SIG developed the research method; all authors collected and analysed data, and managed the literature searches; LVK performed the gradient analysis; VAA collected data about tree stands. All authors contributed to writing the first draft and to final editing of the manuscript, and approved the final version.

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