Effects of persistent water-table level drawdown on fine-root biomass and production in different site types of a boreal forested peatland

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Abstract

Purpose

In peatlands, fine-root biomass (FRB) and production (FRP) and their depth distribution and plant functional type (PFT) composition are poorly known. We studied the effects of persistent water-table level drawdown on these characteristics in four forested boreal peatland site types that varied in soil nutrient and WTL regimes, ground vegetation and tree stand characteristics.

Methods

FRB was estimated by separating and visually identifying roots from soil cores extending down to 50-cm depth. FRP was estimated using ingrowth cores covering the same depth and the separated roots were identified using infrared spectroscopy.

Results

In both FRB and FRP, the differences between undrained and drained sites were small. In FRB, the clearest differences were seen in the originally wettest site, oligotrophic tall-sedge pine fen, and in the most-nutrient-rich site, herb-rich spruce swamp: in the pine fen FRB was smaller, and in the spruce swamp greater in the drained than in the undrained site. FRP was generally higher in nutrient-poor, pine-dominated sites. The depth distribution of FRB was more superficial than that of FRP, except for the most nutrient-rich spruce swamp. Tree and shrub roots dominated both FRB and FRP, except for the undrained pine fen, where graminoids and forbs dominated. Even there, these PFTs were replaced by trees and shrubs at the drained site.

Conclusion

Fine-root biomass and production vary widely both within and among different types of boreal forested peatlands. Lowering of WTL large enough to support greater-volume tree stands affects FRB and FRP relatively little.

Introduction

Peatlands are a great storage of carbon (C) and peat accumulation is one of the major natural pathways to sequester C from the atmosphere to long-term organic deposits (e.g., Page et al. 2011; Yu 2012). Peatlands are a diverse group of habitats that share just one common feature, an organic soil, peat, or Histosol. Otherwise, they range, in the boreal region, from the extremely low-nutrient conditions of some *Sphagnum*-dominated bogs to the high-nutrient conditions of eutrophic fens, and from the soaking wet flark fens to peatland forests, where the soil water-table level (WTL) can be down to 30 cm below the soil

surface, or even deeper during the growing season (Laine et al. 2004; Maanavilja et al. 2014). In several peatland types, vascular plants are an important component in the vegetation, and thus, roots are a major biomass component and root production is a major C flux (e.g., Mäkiranta et al. 2018; Schwieger et al. 2021). However, there is still very limited information available on root biomass and production in peatlands (Iversen et al. 2018). There is even less information available on how root biomass and, especially, production respond to changes in environmental conditions, such as lowering of the WTL caused by anthropogenic activities or climate change (Boggie 1972; Laiho and Finér 1996; Mäkiranta et al. 2018). Yet, these responses will directly affect the C fluxes into the soil, and thus the soil C balance.

Root characteristics of peatland plants generally depend on the plant functional type (PFT) and the environmental conditions such as WTL (e.g., Metsävainio 1931; Proctor and He 2019), these two factors also being strongly correlated (Korrensalo et al. 2017). WTL defines the extent of the oxic layer in the soil. Under wet conditions where the oxic layer is thin, the vascular plants present, such as sedges, have adaptations that enable them to have functioning roots deep in the anoxic soil (Saarinen 1996). Many other plants, including most trees and shrubs, do not tolerate constantly anoxic soil conditions, with their presence restricted to dry sites or microforms, and their roots concentrated on the oxic layer of the soil (Baker et al. 2001). Root litter inputs directly into the anoxic soil layers may contribute significantly to soil C sequestration (Saarinen 1996). In the oxic layers, litter quality determines the rate of organic matter decomposition (Straková et al. 2012). Litter quality largely depends on the plant species or PFT (Straková et al. 2010; Smith et al. 2014; Wulfschleger et al. 2014). The combination of litter quality and thickness of the oxic layer thus are critical for the soil C sequestration and peat formation. In this context, describing rooting patterns and root PFT composition is important but currently hampered by lack of data.

In boreal peatlands, the environment is undergoing changes caused by the climate change. Depending on the region, climate change may cause not only higher temperatures but also prolonged droughts and altered WTL conditions, causing changes in ecosystem functioning (e.g. Reiche et al 2009; Zhaojun et al. 2011). The changes may occur in species composition, such as shifting from herbaceous species dominated to shrubs and tree species dominated ecosystems (Berg et al. 2009; Kokkonen et al. 2019). Allocation to roots and the rooting depth may then also change (Murphy et al. 2009; Proctor and He 2019). Such changes may have feedbacks to fluxes of C, water, and nutrients. Overall, representation of root dynamics in ecosystem and terrestrial biosphere models is gradually improving, but there is need for further empirical data (e.g., Warren et al. 2015).

We analyzed the impact of lowered WTL, produced by decades-old drainage for forestry, on fine-root biomass (FRB) and production (FRP) in four forested peatland site types, which had different nutrient and WTL regimes, and ground vegetation and tree stand characteristics. We further analyzed the PFT contributions to, the depth distribution of, and the effect of some environmental variables on FRB and FRP. We expected that i) both FRB and FRP would be higher in drained sites where the oxic soil layer, favorable for root growth of a wider selection of species, is generally thicker than in undrained sites, but that there could be different patterns in nutrient-poor versus nutrient-rich sites; ii) contributions of different PFTs to both FRB and FRP would change, as graminoids and forbs that are more abundant in

wetter sites would give way to trees and shrubs that are more abundant in drier sites; and iii) depth distribution of both FRB and FRP would be more superficial in drained sites, as the deep-rooted graminoids and forbs of undrained sites would be replaced by more shallow-rooted trees and shrubs.

Materials And Methods

Study sites and their vegetation characteristics

This study was conducted in Lakkasuo and its neighboring Hanhisuo peatlands (61°48' N, 24°19' E; Fig. SI1) in the municipality of Orivesi in southern Finland. Lakkasuo is a partly drained eccentric boreal raised bog complex with a large lagg area and a wide variety of different site types (Laine et al. 2004). The first drainage operations took place in the western part of Lakkasuo in 1928, and in 1961 the whole eastern part of Lakkasuo was drained, making it possible to study changes caused by drainage on several site types (e.g., Minkkinen et al. 1999). For this study, we chose four pairs of undrained and drained sites (Fig. SI1, Fig. SI2) situated in the close vicinity of long-term monitoring plots (see Laine et al. 2004, Sarkkola and Päivänen 2016). Two site pairs were pine-dominated, nutrient-poor sites, and two were spruce-dominated, nutrient-rich sites. The tree stands in the drained sites had developed from the natural tree stands that had grown at the sites already before drainage.

The site with lowest soil nutrient levels represented a **Dwarf-shrub Pine bog** (DP; Finnish name isovarpuräme, classification by Laine et al. 2012, site types described also in Laine et al. 2004) and its 1961 drained counterpart DPdr. DP sites are ombrotrophic, receiving water and nutrients solely from precipitation, and relatively dry even without drainage. Peat depth in both sites was approximately 2 m (Laine et al. 2004). In the DP site, the tree stand consisted solely of Scots pine (*Pinus sylvestris*; plant names follow WFO 2021 unless otherwise specified) and the ground vegetation was dominated by shrubs such as *Ledum palustre*, *Vaccinium uliginosum* and *Empetrum nigrum*, with some graminoid *Eriophorum vaginatum* and forb *Rubus chamaemorus*. Moss cover was continuous and consisted of species with low nutrient demand such as *Sphagnum fuscum*, *S. medium*, *S. angustifolium* and *Pleurozium schreberi*. In the DPdr site, the tree stand had benefited from the drier conditions and was greater by basal area and volume in comparison to DP. Differences in ground vegetation in comparison to DP were rather minor, with less *Rubus chamaemorus* and *Sphagnum* and more forest mosses such as *Pleurozium schreberi* and *Dicranum sp.*

Table 1 Tree stand basal area, tree stand stem volume, ground vegetation projection cover, mean soil water-table level during the study period (2016-2017), and peat properties in the surface peat (0 - 20 cm) in the sites

DP, Dwarf-shrub Pine bog; TP, Tall-sedge Pine fen; VS, *Vaccinium myrtillus* Spruce swamp; HS, Herb-rich hardwood-Spruce swamp; suffix dr indicates drained site

The second pair of sites was **Tall-sedge Pine fen** (TP; varsinainen sararäme) and its 1961 drained counterpart TPdr. These were minerotrophic oligotrophic sites, receiving ground-water flow from the

surroundings. The peat depth in both sites was approximately 2 m (Laine et al. 2004). The undrained TP had a sparse mixed tree stand with pine as the dominant species with some Norway spruce (*Picea abies*) and downy birch (*Betula pubescens*) (Table 1, Fig. SI2). Ground vegetation consisted of sedges such as *Carex lasiocarpa* and *Carex rostrata*, other graminoids such as *Eriophorum vaginatum*, *Salix* sp. bushes, shrubs such as *Betula nana* and forbs such as *Menyanthes trifoliata*. Moss cover was continuous and consisted of species from *Sphagnum recurvum* coll. The tree stand in TPdr was clearly greater, with pine as dominant tree species with relatively dense spruce and birch undergrowth (Fig. SI2). Some lower canopy trees were dying due to shading by bigger trees and biotic damage related to low soil K pools. Shrubs such as *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Vaccinium uliginosum* covered most of the ground but some pre-drainage species such as *Eriophorum vaginatum* and *Vaccinium oxycoccos* remained in more open locations. Moss cover was almost continuous and consisted of *Polytrichum commune*, *P. strictum*, *Sphagnum angustifolium*, *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum* sp.

The third site pair was mesotrophic *Vaccinium myrtillus* Spruce swamp (VS; mustikkakorpi) and its 1965 drained counterpart (VSdr). In comparison to typical *Vaccinium myrtillus* spruce swamps that commonly have peat depth less than 1 m (Laine et al. 2012), both sites had a relatively thick peat layer: approximately 1.5 m in VS and 1.8 m in VSdr (Laine et al. 2004). In both sites the spruce-dominated tree stand had an irregular mixture of pine and birch (Table 1, Fig. SI2). VS was situated below the esker Vatiharju near a large spring area that provided constant ground-water flow to the site. The tree stand had open patches and showed signs of reduced growth and increased natural mortality. Ground vegetation consisted of shrubs *Vaccinium myrtillus*, *Vaccinium vitis-idaea*, sedges *Carex globularis*, *C. canescens*, and forbs *Rubus chamaemorus* and *Trientalis europaea*. Moss cover was continuous and consisted of *Sphagnum girgensohnii*, *S. russowii*, *S. divinum* Flatberg & Hassel, *S. centrale*, *Pleurozium schreberi* and *Dicranum* sp. The VSdr site was situated on the western side of the esker Vatiharju, in Hanhisuo-peatland. In the VSdr, tree stand growth had been quite high for the climatic zone, even higher than in comparable mineral-soil forests (Sarkkola and Päivänen 2016). The stand had been thinned in 1965, 1987 and 1998, and since 2000 suffered from some storm and snow damages that had mostly reduced the number of birches. Ground vegetation was fairly similar to the VS site (Fig. SI2) but with less *Sphagnum* and more forest mosses such as *Hylocomium splendens*, *Dicranum* sp. and *Pleurozium schreberi*.

The most nutrient-rich site pair was the eutrophic Herb-rich hardwood-Spruce swamp (HS; ruohokorpi) and its 1928 drained counterpart HSdr. The tree stand in HS was a mixture of spruce, alder (*Alnus glutinosa*), birch and pine (Table 1, Fig. SI2). In the HS site the peat layer was approximately 1 m thick (Laine et al. 2004), and the site received constant strong ground-water flow from the nearby spring area in the esker Vatiharju (Fig. SI1). The ground was very uneven with trees growing on drier hummocks with wet depressions in between. The vegetation in the hummocks consisted of species such as *Vaccinium myrtillus*, *V. vitis-idaea* and *Trientalis europaea*, whereas forbs such as *Calla palustris* and *Lysimachia thyrsiflora* characterized the depressions. Moss cover was patchy and consisted of forest mosses such as *Dicranum* sp. and *Pleurozium schreberi* in the hummocks and *Sphagnum centrale*, *S. girgensohnii*, *S. squarrosum* and several species of the order Bryales in the depressions. The HSdr tree stand had the

highest volume of all the eight sites and was dominated by spruce with a notable mixture of birch and alder (mostly *Alnus glutinosa*, with some *Alnus incana* (Table 1, Fig. SI2). peat layer was around 0.5 m thick. The dense canopy shaded the ground so that ground vegetation was sparse, consisting of forest species such as *Oxalis acetosella*, *Maianthemum bifolium*, *Calamagrostis arundinacea* and *Vaccinium myrtillus* with some large ferns like *Athyrium filix-femina* and *Dryopteris expansa*. Moss cover was very patchy consisting of forest species such as *Dicranum sp.* and *Pleurozium schreberi*.

In each of the eight sites, we established three plots with three subplots in each, i.e., altogether 24 plots and 72 subplots. Tree-stand basal area and stem volume per species, and projection cover of ground vegetation per species were determined in each plot in summer 2018, except for the VSdr site, which was accidentally clear-cut in spite of on-going research and the ground tilled with an excavator in February 2018. We have thus used tree stand data for this site from a previous survey in year 2010 (Sarkkola and Päivänen 2016), but detailed ground vegetation data is lacking. For the other sites, species data are available in Lampela et al. (202x data, *submitted to PANGAEA*).

Fine-root biomass (FRB)

We focused on fine root biomass (FRB), fine roots generally defined here as roots with diameter ≤ 0.5 mm. All the graminoid, herb and dwarf-shrub fine roots fitted into this category except for the graminoid *Eriophorum vaginatum*, which typically has somewhat thicker roots (e.g., Proctor and He 2019), but was here included in FRB. To cover the varying diameter definitions applied for fine roots (Addo-Danso et al. 2016 and references therein), we also studied diameter classes 0.5–1 mm and 1–2 mm for tree roots (< lower limit, $\leq$ higher limit). The rhizomes of the dwarf-shrubs were not included. Our methods did not facilitate studying intact root systems, which is why we were not taking advantage of the recent developments in fine root classification based on functionality (McCormack et al. 2015; 2017; Ma et al. 2018).

To estimate the living fine root biomass (FRB) *in situ* in the eight sites, we took peat cores from soil surface down to 50 cm depth in late August, 2016, one core from each subplot, altogether nine cores per site and 72 cores in total. We used a box-shaped 65 mm x 37 mm peat corer, except in the wet TP site where we used a 60 mm x 60 mm corer because of difficulties in successfully recovering the wet fibrous peat with the smaller corer. The cores were divided into five 10 cm long segments and stored in freezer for further treatment.

In laboratory, the segments were taken to defrost in refrigerator for approx. 12 hours. We separated the living roots from the peat and dead roots and root sections with tweezers under a magnifying glass. The living roots were divided to the different diameter classes, and to species or species group based on visual identification (see specific section below). The distinction between living and dead roots was done based on the color and elasticity of the root by pulling them with the tweezers. The living roots were dried in 40°C for at least 72 hours and weighed. The values were transformed to per m² using the surface area of the cores.

Fine-root production (FRP)

To study fine-root production (FRP), we used the ingrowth core method (e.g., Milchunas 2009; 2012). We used ingrowth cores that were 50 cm long and approximately 3 cm in diameter, following Laiho et al. (2014) and Bhuiyan et al. (2017). The cores were made of polyester fabric with mesh size approximately 1 mm x 1 mm. We filled the cores with root-free peat matching the peat of the study sites: non-fertilized horticultural *Sphagnum* peat for the nutrient-poor DP sites (bogs), typical sedge peat collected from a site representing the same site type for TP sites (fens), and dark more decomposed swamp peat for the VS and HS sites (swamps).

In each subplot we installed two ingrowth cores, altogether 18 ingrowth cores per site and 144 in total. The cores were installed with a two-piece corer-installer described in Laiho et al. (2014) and expected to reduce the disturbance in the ambient soil as compared to traditional coring. The cores were incubated for two years, as recommended by Bhuiyan et al. (2017) for forested peatlands, starting in November 2015 and ending in November 2017. When recollecting the cores, some broke or were damaged so that we could not include them in the analyses. In the HS site, a storm event in the middle of the incubation period uprooted several trees and simultaneously lifted and destroyed several cores. The number of cores eventually used in the analyses thus varied among sites and was 14 in DP, 16 in DPdr, 16 in TP, 18 in TPdr, 14 in VS, 16 in VSdr, 9 in HS and 17 in HSdr. The collected cores were stored in freezer for further treatment.

In laboratory, the ingrowth cores were taken to defrost in refrigerator for approx. 12 hours, and then cut into 10 cm segments. The diameter of each segment was measured from two angles from both ends, and the average was used for calculating the surface area. Roots were separated from peat with tweezers under a magnifying glass. All roots found in the cores were < 0.5 mm in diameter. There were few dead roots as short segments attached to living roots, and they were not separated since all roots inside the cores represent production during the incubation period. The roots were dried in 40°C for at least 72 hours and weighed. To obtain the annual FRP ($\text{g m}^{-2} \text{ year}^{-1}$) for each core, we divided the dry mass by two (years; incubation time) and by the surface area of the cores.

Identification of the species and species groups

The identification of the plant species of the roots in the FRB samples was done by comparing them with several plant specimens collected from the study sites and stored in alcohol. In most cases there were also some plant remains and living plants with roots still attached on the surface of the uppermost sample (0-10 cm from the peat surface) that helped the identification. In some cases, identification was not possible to species level but only to species group level. This was the case especially in the smallest diameter group (< 0.5 mm) of conifers, certain shrubs (*Vaccinium sp.*, *Ledum palustre* and *Andromeda polifolia*, *Carex sp.* and ferns. In any case, species level data were also pooled into plant functional types (PFTs) for easier presentation of the results and comparison with the FRP data. The PFTs were: i) conifers, ii) birch, iii) alder, iv) shrubs, v) graminoids and vi) forbs.

For the FRP samples, we used Fourier transform infrared spectroscopy (FTIR) to estimate the relative abundance of the PFTs using calibration models developed by Straková et al. (2020). For that, the

separated roots were powdered with an oscillating ball-mill MM400 (Retsch, Germany) and FTIR spectra were measured with a Bruker VERTEX 70 FTIR spectrometer (Bruker Optics, Germany) with a horizontal diamond ATR sampling accessory. In several cases the amount of root material in one segment was so low that we had to combine depth segments from the same core. We will thus present the PFT data at the level of the ingrowth core, without depth information. The calibration models were created using calibration data consisting of known identity root samples. The calibration samples included 22 species common in Finnish peatlands (trees: *Pinus sylvestris*, *Picea abies*, *Betula pubescens*; shrubs: *Andromeda polifolia*, *Betula nana*, *Calluna vulgaris*, *Empetrum nigrum*, *Ledum palustre*, *Vaccinium myrtillus*, *Vaccinium oxycoccos/microcarpum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*; graminoids: *Carex lasiocarpa*, *C. rostrata*, *Deschampsia flexuosa*, *Eriophorum vaginatum*, *Trichophorum cespitosum*; forbs: *Dryopteris carthusiana*, *Epilobium angustifolium*, *Equisetum fluviatile*, *Menyanthes trifoliata*, *Rubus chamaemorus*). The calibration models were designed to quantify the mass proportions of PFTs i) conifers, ii) shrubs and birch, iii) graminoids and iv) forbs. These PFTs were chosen since their fine roots could be distinguished from each other chemically and quantified in composite samples with RMSE generally < 10% (Straková et al. 2020). The forb *Rubus chamaemorus* had to be included in the PFT shrubs and birch, as its FTIR-derived fine-root chemistry is similar to those (Straková et al. 2020). The models are able to predict also the occurrence of such members of PFTs that are not included in the calibration data (Straková et al. 2020).

Environmental variables

Temperature, precipitation, and water-table level

Air temperature and precipitation data were available from the nearby Hyytiälä weather station. We monitored the soil water-table level (WTL; distance, cm, of the water-table from peatland surface) and soil temperatures in 5 and 30 cm depths in each subplot with dataloggers (WTL: Odyssey Capacitance Water Level Logger, Dataflow Systems Limited; T: i-Button DS1921G, Maxim Integrated Products). Hourly data was averaged to daily values. From the daily temperature data, we calculated the temperature sum for years 2016 and 2017 using 5°C as the threshold temperature.

During the incubation period (Nov. 2015–Nov. 2017) the mean air temperature was + 4.3°C and the mean annual precipitation approximately 690 mm. Even though the differences in the annual temperature and precipitation between the two years were small, the growing seasons 2016 and 2017 were far from similar: in 2016 the temperature sum was 1280 d.d. (degree days, >5°C) whereas in 2017 it was only 977 d.d. This difference was also reflected in soil temperatures and soil temperature sums that were lower in 2017 than in 2016 (Fig. SI3). Differences in soil temperature sums between the sites were relatively small. Soil temperature sum in the 5 cm depth was highest in the poorest sites and declined towards the richer sites.

WTL was generally less variable and closer to peat surface in the undrained sites, especially in the TP, VS and HS sites (Fig. 1, Table 1). WTL loggers were inserted to locations that represented the soil surface elevation of the trees. In DP, TP, and VS sites the variation in topography was small and the WTL data is

representative for the whole sites. The HS site, instead, had a higher topographical variation from hummocks with trees to pools with grasses, forbs, and sedges. Thus, as the loggers were located in the hummocks, the WTL data at the HS site represents about 15 cm higher ground (and 15 cm deeper WTL) than that of the pools. The poorest DP site was drier than the other undrained sites and had relatively low mean WTL and variation in the WTL, resembling the drained sites. In the drained sites the WTL was more variable than in the undrained sites throughout the measurement period.

Peat properties

Peat properties of the sites (Table 1) were determined from peat cores taken with similar corers as the FRB samples. One core was taken for this purpose from each plot in each site. The cores were divided into 10-cm segments from soil surface to 50 cm depth. Peat pH of each segment was measured with a Radiometer PHM 82 electrode from fresh subsamples mixed with water to 1:3 ratio suspensions. The segments were then dried at 70°C and weighed. Dry matter content of the segments was measured from subsamples dried at 105°C, and the peat mass were corrected accordingly (also taking into account the pH subsample) for calculation of bulk density as dry mass per fresh volume. For nutrient analyses, the segments representing the same depths from the 3 plots per site were combined and homogenized by milling. Carbon (C) and nitrogen (N) concentrations were determined with combustion method (Vario MAX CN). After dry ashing and HCl digestion, phosphorus (P) was determined spectrophotometrically with the molybdenum blue method (Shimadzu UV-2401 PC) and potassium (K), calcium (Ca), magnesium (Mg) and iron (Fe) with atom absorption spectrometer (Varian AA 240 FS).

In peat properties, the differences between the sites were clear (Table 1). Bulk density increased towards the more nutrient-rich sites and was higher in the drained sites compared to their undrained counterparts, except in the VS pair where the mean BDs did not differ significantly. Soil pH ranged from 4.0 in the DPdr to 5.5 in the HS. In each pair, the undrained site had higher pH than its drained counterpart. Ash percentage increased from the nutrient-poor sites towards the nutrient-rich sites, and the drained sites had a higher ash % than their undrained counterparts, except for VS. Concentrations of mineral nutrients generally increased from the poor sites towards the rich sites. C/N ratio was highest in the nutrient-poor DP sites and in each pair higher in the undrained site than in the drained site.

Data analyses

To estimate the standard error of the mean FRB and FRP for each site, taking into account the clustered sampling, we used linear mixed models. In these models, the plots were accounted for in the random part of the model in the following way:

$$\text{FRB}_{ij} \text{ or } \text{FRP}_{ij} = \beta_0 + u_j + \varepsilon_{ij}$$

where β_0 is the intercept or mean of FRB or FRP, u_j is a random variable describing the cluster level (=plot) variation that follows the normal distribution $\sim N(0, \sigma^2_{\text{plot}})$ and ε_{ij} is the residual $\sim N(0, \sigma^2)$.

We explored the overall differences in the FRB and FRP between the eight sites with one-way ANOVA. In case of a significant site effect, we tested the differences between the undrained and drained sites of each site pair with independent samples t-tests.

For studying the effects of site characteristics and environmental variables on the FRB and FRP, we used linear mixed models. Similar models were tested for total FRB, FRB of tree species and PFTs, total FRP and FRP of PFTs. The tested models were 3-level models, where FRB or FRP from each core was set as a response variable that was nested within a plot, nested within a site. Subplot level was not included in the models since it was not available in the FRB and was available only in part of the FRP plots. The explanatory environmental variables (fixed effects) were measured either on plot or site level. The tested variables were: tree stand basal area (plot level), species-specific basal areas of pine, spruce, birch and alder (plot level); % coverage of shrubs, graminoids and forbs (plot level); WTL (plot level): i) means of time periods covering the two growing seasons during the incubation period from May to October in 2016 and 2017, ii) mean of July-August in 2016 and 2017 and iii) 10th and 90th percentiles of WTL during the incubation period from Nov. 2015 to Nov. 2017; mean soil temperature sum of years 2016 and 2017 in 5 cm depth (plot level); pH, bulk density (plot level; means for 0-50 cm); ash %, C/N ratio, phosphorus, potassium, calcium, magnesium and iron (site level; means for 0-50 cm). The model was as follows:

$$\text{FRB}_{ijk} \text{ or } \text{FRP}_{ijk} = \beta_0 + \beta_1 * \text{env}_k + \dots \beta_n * \text{env}_k + \beta_2 * \text{env}_{jk} + \dots \beta_n * \text{env}_{jk} + u_k + u_{jk} + \varepsilon_{ijk}$$

where β_0 is the overall intercept of the FRB or FRP; $\beta_1 * \text{env}_k + \dots \beta_n * \text{env}_k$ represent the fixed effects associated with the environmental variables in the site level k ; $\beta_2 * \text{env}_{jk} + \dots \beta_n * \text{env}_{jk}$ represent the fixed effects in the plot level j ; the u_k is a random effect associated with the intercept for site k that follows the normal distribution $\sim N(0, \sigma^2_{\text{intercept:site}})$; $u_{jk} \sim N(0, \sigma^2_{\text{intercept:plot}})$ is a random effect associated with a plot j nested within site k ; and $\varepsilon_{ijk} \sim N(0, \sigma^2)$ represents the residual variance associated with the core level (ingrowth core or peat core used for biomass determination). The model formulation and selection of the best model was done by following the procedure described by West et al. (2014) for three-level models for clustered data, where we used the -2 restricted log-likelihood scores to select the best models with maximum likelihood estimation (ML). After the best model for a selected response variable was found, we used restricted maximum likelihood estimation (REML) to derive the final parameter values.

All statistical analyses were performed by using the IBM SPSS Statistics version 25.

Results

Fine root biomass (FRB)

Variation in FRB (diameter < 0.5 mm) between individual cores was high, with the lowest FRB in one core found in HS (33 g m⁻²) and the highest in HSdr (785 g m⁻²). The lowest mean FRB of the eight sites was 121 g m⁻² in the TPdr site and the highest 342 g m⁻² in the HSdr site (Fig. 2). In the pine-dominated, nutrient-poor sites (DP and TP), the drained sites had on average lower total FRB than the undrained sites,

while the opposite was true for the spruce-dominated, nutrient-rich sites (VS and HS) (Fig. 2). Pairwise differences were significant only for TP and HS (Table SI1a).

The species composition of FRB varied considerably among the sites (Fig. 2). Tree roots dominated in FRB at all but the TP site, where most of the FRB were of sedges (*Carex sp.*). Also, forbs such as *Menyanthes trifoliata* were abundant at TP. This dominance of sedges and forbs in TP changed to dominance of arboreal roots in the drained TPdr. In DP, DPdr, HS and VS sites, shrubs formed a notable part of the FRB. In the nutrient-rich drained sites VSdr and HSdr, the biomass of conifer roots was significantly higher than in their undrained counterparts.

In general, the FRB of the different tree species reflected the basal areas of the same species in the sites (Fig. 2, Table 1). There were, however, some minor inconsistencies. For example, there was a small amount of spruce in TPdr (basal area $2 \text{ m}^2 \text{ ha}^{-1}$), but no spruce roots were found in the biomass cores. In HS on the other hand, no pines occurred in the stand measurement plots, but some roots were identified as pine roots. There can be some occasional small pines in this site type, thus this inconsistency can be coincidental.

Examining the relation of the total FRB with environmental variables gave meager results (Table SI2). Only the basal area of alder (present only in the HS and HSdr sites) had a significant, positive correlation with total FRB. The basal area of spruce had a slight negative correlation with the FRB on conifers. The basal areas of birch and alder had a positive correlation with the FRB of the grouped shrubs and broadleaf trees, whereas the correlation with the coverage of graminoids was negative. The coverage of graminoids had a positive correlation with the FRB of both graminoids and forbs. Soil temperature in 5 cm depth and C/N ratio both had a slight positive correlation with the FRB of shrubs.

Including roots up to diameter 2 mm changed the picture, especially for the TP pair (Fig. 3, Table SI1b). TP had very little other than the smallest diameter class roots in comparison to the drained site where bigger-diameter tree roots were abundant, so that the total FRB of roots $\leq 2 \text{ mm}$ were quite similar in TP and TPdr. In the other pairs, the differences between the undrained and drained sites regarding diameter classes were smaller.

FRB declined in all sites from the 0-10 cm peat layer downwards (Fig. 4). In all DP and VS sites, as well as TPdr, FRB was concentrated in the topmost 10 cm layer with almost no roots below 20 cm depth. In TP and both HS sites, FRB declined more gradually from the surface towards deeper layers so that there were still notable amounts of roots in the 30 cm depth.

The FRB depth distribution of species and PFTs varied between sites (Lampela et al. 202x data). In the DP and DPdr sites, shrubs and the graminoid *Eriophorum vaginatum* were the only species reaching the deepest, 40-50 cm, layer studied. In TP, there were both graminoids and forbs in the deepest layer, but in TPdr no roots at all in the deepest layer. In VS some forb and graminoid roots were found in the deepest layer of one subplot, whereas the roots of pine and forbs reached to the deepest layer in VSdr. In both HS

and HSdr there were alder and pine roots in the deepest layer, whereas spruce and birch roots were found in the 30-40 cm depth only in HSdr.

Fine root production (FRP)

Variation in FRP between individual cores was high, one core at VS lacked roots altogether whereas the highest FRP in one core was $300.4 \text{ g m}^{-2} \text{ year}^{-1}$ at DP. Mean FRP varied from $30.7 \text{ g m}^{-2} \text{ year}^{-1}$ at HSdr to $119.9 \text{ g m}^{-2} \text{ year}^{-1}$ at TPdr (Fig. 5). There were no significant differences in total FRP between the undrained and drained sites in any of the site pairs (Table S11c).

Tree and shrub roots dominated in the FRP, except in TP where graminoids had the biggest share (Fig. 5). FRP of forbs was minor at all sites. When comparing the undrained and drained sites, TP had significantly less FRP of conifers, shrubs and broadleaf trees, and more FRP of graminoids than TPdr (Fig. 5). In HS, shrubs and broadleaf trees had more FRP than in HSdr, whereas DP and VS showed no differences between the undrained and drained sites. *Rubus chamaemorus* was grouped together with shrubs in FTIR analyses, thus there appears to be no forbs at DP sites where this was the only forb species present.

Of the tested environmental variables, only two had significant correlation with the FRP (Table S2): Pine basal area correlated positively with total FRP, FRP of conifers, and FRP of shrubs and broadleaf trees, and – self-evidently – the coverage of graminoids had a positive correlation with FRP of graminoids and forbs.

FRP declined from the topmost 0-10 cm layer towards deeper layers at all sites except TP where the highest mean FRP was found in the 10-20 cm depth (Fig. 6). The TP sites showed higher FRP in deeper layers than the other sites, and a notable amount of roots even in the 40-50 cm depth. At all VS and HS sites, FRP was concentrated in the topmost 20 cm with sharp decline towards the deeper layers.

Comparisons between FRB and FRP

Generally, variation was high in both FRB and FRP and few significant patterns emerged. The most evident difference appears to be that FRP was generally lower in the nutrient-rich VS and HS sites whereas FRB showed no such general pattern (Figs. 2 and 5). Intriguingly, the highest mean FRB was found in the drained nutrient-rich HSdr site and lowest in the drained nutrient-poor TPdr site, while in the FRP the pattern was exactly the opposite.

The PFT distribution generally followed similar patterns in both FRB and FRP. The most notable exception was the proportion of graminoids that was generally higher in FRP, except in TP, where it was lower in FRP. The share of conifers was somewhat higher in FRB in all sites but TP and HS. In HS, the share of shrubs and broadleaf trees was higher in FRB. The depth distribution of FRB was more superficial than that of FRP, except for the HS sites (Fig. 7).

Discussion

As far as we know, this was the first comprehensive survey of the effects of WTL drawdown on the patterns of fine-root biomass (FRB) and fine-root production (FRP) covering several peatland site types. In both FRB and FRP, the differences between undrained and drained sites were surprisingly small in the forested peatland types that we studied. In FRB (diameter ≤ 0.5 mm), the clearest changes were seen in the two wettest sites, Tall-sedge Pine fen (TP) and Herb-rich hardwood-Spruce swamp (HS), where also the contributions of different plant functional types (PFTs) changed the most. In the nutrient-rich HS, the increase in tree FRB following WTL drawdown was more than enough to compensate for the reduction of FRB in species adapted to wet conditions, while in the nutrient-poor TP, this was not the case. In the two other, drier, site types, trees dominated FRB already in the undrained sites, with only small changes in the amount and PFT composition of FRB.

In FRP, the clearest pattern was the generally higher production in the nutrient-poor, pine-dominated sites. Our results thus suggest that in nutrient-rich peatlands, less FRP may be needed for nutrient acquisition than in nutrient-poor sites. The number of sites is limited, however, so results from a larger sample of sites are needed for stronger conclusions.

Overall, FRB and FRP were not always fully coupled, but could respond in opposite ways to WTL drawdown. This is, as such, not odd, as FRB may better reflect occupation of available space while FRP may better reflect investment into nutrient acquisition. Depth distribution of FRB and FRP also differed to some extent, suggesting that explorative roots may be produced deeper down than where conditions for longer-term root survival are generally found. In all sites with predominantly tree and shrub roots (i.e., all but TP), roots were more superficially distributed than the average for boreal forests (Schenk and Jackson 2002), reflecting the general importance of the WTL in controlling rooting depth in peatland forests.

The study sites varied widely in the measured vegetation parameters and environmental variables, as is typical for boreal forested peatlands (e.g., Laine et al. 2004). They varied from sparse to full tree canopy cover, and ground vegetation was equally versatile ranging from dense shrub or sedge cover to patchy cover of mosses under the densest tree stand. Also, the WTL and nutrient regimes varied. There are thus numerous factors potentially affecting the FRB and FRP in these sites. Accordingly, the variation in all features of FRB and FRP was high. Thus, statistically significant patterns were scarce and the confidence intervals of the estimates wide. High spatial variability in root biomass and production is common in different environments and planning a sample size big enough to gain reliable estimates can be challenging (Berhongaray et al. 2013).

The overall level of FRB was comparable to previous results from both drained peatlands and mineral soil forests (Vogt et al. 1995; Borken et al. 2007; Finér et al. 2011; Brunner et al. 2013; Lehtonen et al. 2016). The FRP in the nutrient-poor sites was similar to FRP reported for similar sites by Finér and Laine (1998, method I) and Finér and Laine (2000), but lower than that reported by Finér and Laine (1998, method II) and Bhuiyan et al. (2017). For the nutrient-rich sites, there are little earlier published FRP results for

comparison, but the FRP of 560 g m^{-2} estimated by Bhuiyan et al. (2017) with the same method for a pine-dominated nutrient-rich site is tenfold higher than our estimates that ranged $30\text{-}70 \text{ g m}^{-2}$. FRP estimates vary depending on the estimation method, ingrowth cores generally yielding lower FRP estimates than, e.g., minirhizotrons (e.g., Hendricks et al. 2006; Milchunas 2012); however, this has not been confirmed for total FRP (trees + ground vegetation) in forests (Finér et al. 2011).

We had only one site representing one site type and drainage status, and thus can draw limited inference on site-type related phenomena. However, the data revealed several interesting patterns, but also indicated some potential problems in our methodology. Responses – or the lack of those – of both FRB and FRP to the WTL drawdown varied among site types and reflected the original (undrained status) WTL and nutrient regimes. In peatlands, these two regimes largely determine the PFT composition that is the mediator of the responses (Korrensalo et al. 2017). Many PFTs are adapted to specific conditions, and when the conditions change, the PFT composition usually changes (Laine et al. 1995; Weltzin et al. 2003; Breeuwer et al. 2009; Munir et al. 2014; Churchill et al. 2015; Kokkonen et al. 2019). When one PFT suffers, another PFT may occupy its space, and compensate for the reduction in biomass and/or production of the receding PFT (Weltzin et al. 2000; Korrensalo et al. 2017; Mäkiranta et al. 2018). This was well evident in TP, our wettest site type that showed the strongest response to WTL drawdown.

Under the wet conditions of TP, both FRB and FRP were dominated by graminoids. Trees and shrubs in this site type are usually found on slightly elevated hummocks that offer better soil aeration. For trees, the conditions are in any case challenging, as shown in low tree basal area. The graminoids in TP were largely sedge species (Lampela et al. 202x data) that tolerate anoxic soils thanks to their aerenchymous root systems (e.g., Visser et al. 2000). These root systems allow oxygen transport to roots as deep as two meters below the soil surface (Saarinen 1996). In TP, the share of conifers was much higher in FRP than in FRB, unlike in any other site, which could indicate that these presumably highly stressed plants had to renew their fine roots faster than the plants better adapted to the site conditions. Another explanation would be that tree roots would have colonized the ingrowth cores faster than sedge roots, but this is unlikely since the opposite has been observed earlier (Finér and Laine, 2000).

At TPdr, all sedge and forb species adapted to wet conditions were completely lacking, as is commonly the case following persistent WTL drawdown (e.g., Laine et al. 1995). Interestingly, this affected overall FRB but not FRP. The lower graminoid FRP was compensated for by higher FRP of trees and shrubs. Also, the FRB of trees and shrubs was higher, but not as much as the FRB of graminoids was lower than in TP. Yet, when including fine roots up to the diameter of 2 mm, also FRB was similar to that of TP. This investment in longer-living roots in the drained conditions probably partly just reflects the overall larger tree stand, but may also be linked to the need to expand the rooting system to support the increased aboveground biomass in the TP deep-peat conditions. Earlier observations of relatively higher coarse root biomass in peatland versus mineral-soil pine stands may support this assumption (Laiho and Finér 1996).

In the Dwarf-shrub Pine bog (DP) site pair, in contrast, there was no difference between the undrained and drained site in either FRB or FRP. This site type is relatively dry to begin with and has low peat pH and nutrient concentrations. Consequently, there is little chance for a major vegetation change, since the plant species that are competitive in these conditions are limited and they are already present in the undrained site. Generally, the response of vegetation composition to persistent WTL drawdown is the faster and more extensive the wetter and more nutrient-rich the site initially is (Laine et al. 1995). The clearly larger tree stand of the DPdr was not reflected in either FRB or FRP. The biomass of tree roots in diameter class 0.5-1 mm was actually lower under the drained condition; we can think of no explanation for this. Similarly to TPdr, conifers showed smaller share in FRP than FRB, indicating slower turnover than shrub and, especially, graminoid roots. The only graminoid found in this site was *Eriophorum vaginatum*, which renews its roots annually (Chapin et al. 1979).

One reason for the small or non-existing differences in FRB and FRP in the ombrotrophic DP site may be that the drained site has become significantly wetter during the last years due to the gradual blocking of the border ditch by mire vegetation. In 1991, the difference in median WTL was clear: 21 cm in the undrained vs. 34 cm in the drained (Minkkinen et al. 1999). Now the difference had almost disappeared: 22 vs. 23 cm in the undrained vs. drained, respectively (Table 1). Similar development has taken place with the TP and TPdr: in 1991 the WTLs were 10 and 41 cm, whereas now they were 13 vs 20 cm in the undrained and drained sites, respectively.

The spruce-dominated *Vaccinium myrtillus* Spruce swamp (VS) and HS site pairs showed many similarities but also some differences. Here the differences in vegetation, tree stand, and peat properties were relatively small between the undrained and drained sites. FRB was predominantly arboreal, and mostly of conifers, except for HS that had a considerable share of alder in the tree stand. The overall shallow fine-root distribution is explained by the lack of deep-rooted graminoids and forbs in these sites.

The extremely low FRP observed for the HSdr site, which showed the highest FRB of all the sites, is surprising. Overall, the FRP in the HS sites was clearly lower than we expected. There may be three explanations for this: i) in these nutrient-rich sites vegetation can forage enough of nutrients even with low FRP; ii) FRP is in fact higher but our method did not capture it in these sites, or iii) our method fails altogether to capture FRP in peat soils. Option iii) seems unwarranted since the FRP estimated for the nutrient-poor sites appeared realistic. Option i) is not in line with the few earlier results from nutrient-rich sites (Bhuiyan et al. 2017) but requires data from a larger set of sites for proper evaluation. For forests on mineral soils, different hypotheses have been presented on the relationship between FRP and soil resource availability (e.g., Hendricks et al. 2006). However, there seems to be no overall consensus of any consistent relationship between FRP and soil nutrient status based on field studies (Hendricks et al. 2006, Yuan and Chen Han 2012). In any case, FRP is also constrained by the tree stand basal area, and FRB (e.g., Finér et al. 2011).

Concerning option ii) there are (at least) three ways in which our measurements could have gone wrong. Even though the installation of the cores is in general very easy with our corer-installer (Laiho et al. 2014),

in sites with high biomass of coarse roots, especially, the “root mat” is not readily penetrated by the corer and thus, the cores could end up being installed in locations with less tree root biomass and potentially also less FRP. Even though the installation was planned as random, we cannot completely overrule this possibility. This could also add to the ground vegetation contribution being higher in FRP than FRB, apart from differences in turnover rates since ground vegetation generally thrives in the more open areas between trees.

Also, the HS sites had the densest peat and the shallowest peat layer, and the drained site was drier than the other sites. Contact between dry peat and ingrowth cores may remain poor, which would hamper root ingrowth. This is one reason why we recommend always installing the cores in the previous autumn, to ensure the formation of seamless contact between the cores and ambient soil (Laiho et al. 2014). Yet, we do not believe that peat contact was the problem here, since recovery of the cores indicated the opposite – it was “hard enough”, while poorly connected cores would be easy to pull out. However, since all cores were prepared to the same length, in these sites a higher proportion of peat-filled core remained on top of the peat surface. That could potentially result in capillary drying of the core peat during the summer, resulting in smaller-than-ambient root growth.

Yet another potential factor is the quality, especially nutrient content of the peat used as substrate in the cores. We did not use peat from the sites but tried to find standard peat types that would match the peat of the sites. Unfortunately, we did not measure the peat quality extensively before use. In retrospect, we can conclude that the success varied. The clearest failure was the swamp peat used for the nutrient-rich spruce sites (VS and HS pairs). This peat turned out to have much lower phosphorus (P) concentration than the peat at the sites (Supplementary Fig. SI4.). This may have led to lower-than-real FRP estimates, since P is often the limiting nutrient in forested peatlands, alone or together with potassium (K) (e.g., Moilanen et al. 2010, Hill et al. 2014). K concentration is thus also important, and challenging to manage, since the peat K is mostly soluble and in deep-peated sites shows a sharp decline from the topmost peat downwards (e.g., Laiho et al. 1999). This is impossible to reproduce with standard peat, and challenging also with peat from the site. This is another reason why we recommend always installing the cores in the previous autumn, so that biological processes could start to shape the K profile.

In the recovered cores, the K profile had to some extent developed towards the natural shape. Yet, the cores still had lower K concentrations than the ambient peat in the topmost layer in all sites, and higher in the three lowest layers in the DP and TP pairs. This may in principle have reduced FRP in the topmost layer(s) but enhanced FRP in the deeper layers and contributed to the pattern of FRB being more superficial than FRP. Still, all FRP in the deeper layers must have come from live root biomass in those layers since no vertical root growth inside the cores was observed, which speaks against a K-induced artefact there.

The success in matching nutrient concentrations further varied between undrained and drained sites, the concentration patterns being better matched in the drained sites. This implies that different peat should be used for undrained and drained sites in studies including both. Naturally, the best option would be to

collect peat for the ingrowth cores (layer-wise) from the very sites at which the cores will be incubated. How much the nutrient contents in the ingrowth cores actually affected root growth and the FRP estimates is difficult to evaluate without cores with various peats installed at the same site. The within-site variation in peat nutrient concentrations is high (Laiho et al. 2004), and our data for both the ambient and ingrowth-core peats is limited. Also, the availability of K, especially, that is mostly soluble (Starr and Westman 1978), moves readily with water, including e.g., throughfall (), and is tightly cycled where scarce (e.g., Stone and Kszystyniak 1979), may not be perfectly described by one-time sampling. There are earlier observations that higher nutrient concentrations inside ingrowth cores may, to a varying extent, increase root ingrowth (Raich et al. 1994; Steingrobe et al. 2000), and it thus seems well possible that lower concentrations would reduce ingrowth.

The depth distribution of FRB and FRP was mainly related to the species composition and the WTL in the site. In the undrained sites with high WTL, there were species adapted to anoxic conditions, such as sedges and the forb *Menyanthes trifoliata*, that are known to have deep roots (Sjörs 1991; Kohzu et al. 2003). Of trees, alder, pine and birch had some roots in the deeper layers also in the undrained sites, which was somewhat unexpected, whereas spruce roots were concentrated in the topmost layers. When peatland is drained, the oxic layer in peat extends deeper and creates space for aerobic processes. This did not, however, lead to deeper rooting depth in this study. Also, in more extensive studies on the effect of peatland forest drainage on rooting depth, it has been found that the impact is minor (Paavilainen 1966), about 1 cm difference of rooting depth in 10 cm difference in WTL (Heikurainen 1955). It should be noted here that the differences in the WTL between the undrained and drained sites were overall rather modest. Relatively high WTLs are common in boreal extensively managed drained sites (e.g., Ojanen et al. 2010 Fig. 6). In deeply drained sites, tree roots can extend deeper than in our sites (Holmen 1964).

The interactions of the variables studied are complex, and thus chances for successful modeling of FRB or FRP in a dataset as varied as ours are quite limited. For instance, differences in the soil temperature between our sites were relatively small and generally related to the shading and cooling effect of the tree stand, so that the highest soil temperatures were found in the nutrient-poor DP sites with the smallest tree stands. The temperature-related higher biological activity that could enhance root growth (Alvarez-Uria and Körner 2007; Malhotra et al. 2020) was thus in our data set probably overridden by other tree stand effects. Further, the WTL that is a critical constraint for most features of peatland ecosystem structure and function, including root systems (e.g., Lieffers and Rothwell 1987; Murphy et al. 2009), simultaneously affects so many parameters that extracting its pure impact in a data set as varied as ours is not in practice feasible. That the environmental variables had little effect in our models agrees with findings for forests on mineral soils (e.g., Finér et al. 2011).

Our results revealed what probably could be expected – that fine-root biomass and production vary widely both within and among different types of boreal forested peatlands. They further highlight some challenges in using peat-filled ingrowth cores. Even though it is common these days to request straightforward conclusions from all individual studies, we do not despair in front of the diversity of the results: we believe that they reflect quite well the inherent diversity and heterogeneity of peatlands, which we also

wish to emphasize. It is critical to note that a pattern nicely observed in one peatland site and one method is not necessarily repeated elsewhere, and no firm conclusions should be based on results from a limited number of sites. Even though root studies are laborious and methodologically challenging, the research community should aim to gradually build up a data base for forming a realistic bigger picture of the rooting patterns and the related carbon fluxes in peatlands.

Data Availability

The data used in this article have been submitted to PANGAEA and are currently being processed. A link will be added to the manuscript after it has been accepted for publication.

Declarations

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Statements and Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author contributions

This research was designed by Kari Minkkinen, Timo Penttilä and Raija Laiho with contributions from Petra Straková, Päivi Mäkiranta and Paavo Ojanen. Material preparation, data collection and analysis were performed by all authors. The first draft of the manuscript was written by Maija Lampela and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Table 1

Table 1 can be found in the supplementary files section.

Figures

Figure 1

Soil water-table level (WTL) in the a) DP, DPdr, TP and TPdr sites and b) VS, VSdr, HS and HSdr sites during the ingrowth-core incubation period from November 2015 to November 2017. DP, Dwarf-shrub Pine bog; TP, Tall-sedge Pine fen; VS, *Vaccinium myrtillus* Spruce swamp; HS, Herb-rich hardwood-Spruce swamp. Suffix dr indicates drained site. Please note that the measurements for HS represent hummocks and not the average of the site as for the other sites.

Figure 2

Mean total fine-root biomass (FRB, g m^{-2} , diameter ≤ 0.5 mm) and its plant functional type (PFT) composition in the sites. Error bars represent standard error of the mean. Stars on top of the bars indicate significant difference in total FRB between the undrained and drained sites of a site type pair. A star inside a stack indicates a significant difference in the FRB of that PFT between the undrained and drained sites of a site pair. PFT identification was done visually. DP, Dwarf-shrub Pine bog; TP, Tall-sedge Pine fen; VS, *Vaccinium myrtillus* Spruce swamp; HS, Herb-rich hardwood-Spruce swamp. Suffix dr indicates drained site.

Figure 3

Mean fine-root biomass (g m^{-2} , SE in error bars) including tree roots up to diameter 2 mm in the sites. Other species includes all graminoid, shrub and forb fine roots. A star inside a stack indicates a significant difference in a biomass component between the undrained and drained sites of a site pair. DP, Dwarf-shrub Pine bog; TP, Tall-sedge Pine fen; VS, *Vaccinium myrtillus* Spruce swamp; HS, Herb-rich hardwood-Spruce swamp. Suffix dr indicates drained site.

Figure 4

Depth distribution of fine-root biomass (FRB, g m^{-2} , diameter ≤ 0.5 mm) in each pair of undrained and drained sites representing the same site type. Filled symbol is the undrained, and open symbol the drained site of each pair. Error bars represent SE. Note that the symbols are located in the middle of the 10-cm layers studied. DP, Dwarf-shrub Pine bog; TP, Tall-sedge Pine fen; VS, *Vaccinium myrtillus* Spruce swamp; HS, Herb-rich hardwood-Spruce swamp. Suffix dr indicates drained site.

Figure 5

Mean total fine-root production (FRP, $\text{g m}^{-2} \text{ year}^{-1}$) and its plant functional type (PFT) composition in the sites. Error bars represent SE. A star inside a stack indicates a significant difference within that PFT for the undrained and drained sites of a site pair. PFT identification was based on FTIR spectral analyses. *Rubus chamaemorus* was grouped together with shrubs in FTIR analyses. DP, Dwarf-shrub Pine bog; TP, Tall-sedge Pine fen; VS, *Vaccinium myrtillus* Spruce swamp; HS, Herb-rich hardwood-Spruce swamp. Suffix dr indicates drained site.

Figure 6

Depth distribution of fine-root production (FRP) in each pair of undrained and drained sites representing the same site type. Filled symbol is the undrained, and open symbol the drained site of each pair. Error bars represent SE. Note that the symbols are located in the middle of the 10-cm layers studied. DP, Dwarf-shrub Pine bog; TP, Tall-sedge Pine fen; VS, *Vaccinium myrtillus* Spruce swamp; HS, Herb-rich hardwood-Spruce swamp. Suffix dr indicates drained site.

Figure 7

Mean cumulative proportion of fine-root biomass (FRB, diameter ≤ 0.5 mm) and fine-root production (FRP) from the topmost 0-10 cm layer to deeper layers in each pair of undrained and drained sites representing the same site type. Error bars represent SE. Note that the symbols are located in the middle of the 10-cm layers studied. DP, Dwarf-shrub Pine bog; TP, Tall-sedge Pine fen; VS, *Vaccinium myrtillus* Spruce swamp; HS, Herb-rich hardwood-Spruce swamp. Suffix dr indicates drained site.

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