Cotton-grass and blueberry have opposite effect on peat characteristics and nutrient transformation in peatland

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Author contributions

EK, HŠ and TP conceived and designed the study as well as the field methods, KE sampled plant material and measured decomposition rates in the field and performed language corrections, PS analyzed plant material using IR, JB analyzed enzymatic activities, ZU and JM performed the field and laboratory portion of the research. EK wrote the paper with editorial help of other co-authors.

Cotton-grass and blueberry have opposite effect on peat characteristics and nutrient transformation in peatland

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Abstract

Peatlands are large repositories of carbon (C). *Sphagnum* mosses play a key role in C sequestration, while the presence of vascular plants is generally thought to stimulate peat decomposition. Recent studies stress the importance of plant species for peat quality and soil microbial activity. Thus, learning about specific plant–microbe–soil relations and their potential feedbacks for C and nutrient cycling are important for a correct understanding of C sequestration in peatlands and its potential shift associated with vegetation change. We studied how the long-term presence of blueberry and cotton-grass, the main vascular dominants of spruce swamp forests, is reflected in the peat characteristics, soil microbial biomass and activities, and the possible implications of their spreading for nutrient cycling and C storage in these systems. We showed that the potential effect of vascular plants on ecosystem functioning is species-specific and need not necessarily result in increased organic matter decomposition. While the presence of blueberry enhanced phosphorus availability, soil microbial biomass and the activities of C acquiring enzymes, cotton-grass strongly depleted phosphorus and nitrogen from the peat. The harsh conditions and prevailing anoxia retarded the decomposition of cotton-grass litter and caused no significant enhancement in microbial biomass and exoenzymatic activity. Therefore, the spread of blueberry in peatlands may stimulate organic matter decomposition and negatively affect the C sequestration process, while the potential spread of cotton-grass would not likely change the functioning of peatlands as C sinks.

Introduction

Peatlands are nutrient-deficient systems which can accumulate large amounts of carbon (C) due to slow peat decomposition. This slow rate of decomposition is regulated by the prevailing anaerobic soil conditions and low mean temperatures associated with the high altitudes or latitudes where peatlands are predominantly found (Limpens and others, 2008). *Sphagnum* mosses play a key role in this C sequestration due to the production of decay resistant litter (Hájek and others, 2011). Peat accumulation changes the local hydrology and pore water biogeochemistry, which generally positively feeds back to support *Sphagnum* (van Breemen, 1995). Therefore, *Sphagnum*-dominated vegetation is considered to be fundamental to many ecosystem functions, including C storage (Limpens and others, 2008; Bragazza and others, 2013; Kuiper and others, 2014), providing the stability and resilience of peatland ecosystems (Turetsky and others, 2012).

Besides *Sphagnum* mosses, vascular plants are typical inhabitants of peatlands, with water table, nutrient status and temperature being the dominant factors controlling species composition and biomass (Bragazza, 2006; Breeuwer and others, 2009; Laine and others, 2012; Dieleman and others, 2015). Peatland vascular plants are more efficient photosynthetizers under all light levels than *Sphagnum* mosses (Leppala and others, 2008), enhancing net ecosystem primary production and net CO_2 exchange (Tuittila and others, 1999; Riutta and others, 2007; Laine and others, 2012). Through the labile C released in root exudates, vascular plants shape soil microbial community structure (Bragazza and others, 2015) and their presence can be associated with greater microbial biomass and decomposition activity (Bragazza and others, 2013; Jassey and others, 2013; Bragazza and others, 2015). Moreover, peatland vascular plants contain more N and P in their living tissues in comparison to peat mosses (Wang and Moore, 2014), with a positive effect on the decomposability of their tissues (Hobbie, 1996; Dorrepaal, 2007) and nutrient cycling in peatlands (Jassey and others, 2013; Bragazza and others, 2015).

Most peatland vascular plants belong to two plant functional types, graminoids (sedges) and ericoid shrubs. Deeply rooting graminoids with aerenchyma generally occur in wetter habitats with mean water table ranging from –10 to –20 cm and are strong competitors in such habitats, while ericoid shrubs are abundant further above the water table, avoiding soil anaerobiosis (Bragazza, 2006; Laine and others, 2012). The differing life strategies of the two functional types are connected with differences in their tissue and litter chemistry (Moore and others, 2007; Wang and Moore, 2014). Graminoids have higher photosynthetic capacities and respiration rates (Bubier and others, 2003; Riutta and others, 2007; Leppala and others, 2008) and lower contents of phenolics and lignin in the litter than ericoids (Hobbie, 1996; Dorrepaal, 2007), suggesting their higher tissue decomposability. Moreover, the plant functional types are associated with soil microbial communities of different composition (Haichar and others, 2008; Bragazza and others, 2015; Robroek and others, 2015b). Therefore, the presence of graminoids or ericoids differentially impact net ecosystem CO_2 exchange, its drought response (Riutta and others, 2007; Laine and others, 2012; Kuiper and others, 2014) and CH_4 dynamics (Robroek and others, 2015b; Strom and others, 2015), and very likely also on peat composition, soil microbial biomass and nutrient cycling.

It is expected that changing climate conditions will shift the functional composition of peatland vegetation towards a graminoid-dominated system under elevated temperatures or increased precipitation (Wahren and others, 2005; Dieleman and others, 2015) and towards a shrub-dominated community under a combination of drier and warmer seasons with decreased water levels (Bragazza and others, 2013; Heijmans and others, 2013). Therefore, learning about specific plant–microbe–soil relations and their potential feedbacks for peat quality and nutrient cycling are important for correctly understanding peatland ecosystem functioning as a C sink and its potential shift associated with vegetation change (Heijmans and others, 2013; Bragazza and others, 2015). We found only a few papers about peatlands which investigated the cascade effects of different plant species or plant functional types on the characteristics of soil organic matter and microbial biomass. Bragazza and others (2013, 2015) linked increasing ericoid shrub abundance in peatlands to the structure, C:N stoichiometry and activity of the soil microbial community and dissolved organic matter chemistry, while Robroek and others (2015b) demonstrated a direct effect of the removal of different plant functional types on microbial community composition. Jassey and others (2013) related changes in the peatland vascular plant community resulting from warming effects to the structure of microbial food webs. Recently, Robroek and others (2015a) and Pinsonneault and others (2016) stressed the importance of plant species (or more generally plant functional types) to dissolved organic matter chemistry and its biodegradability, with a possible influence on microbial respiration and dissolved organic matter export from peatlands.

We selected spruce swamp forests (SSF) as a representative type of peatland for the purpose of linking the specific effect of plant species presence on the characteristics of peat and the soil microbial community. SSF are widespread peatland systems, characterized by a patchy distribution of understory vegetation of different plant functional types reflecting site microtopography. In Central Europe and parts of Western Europe, SSF are considered as nutrient poorer types of peatlands because they are located in mountain areas formed by very old, nutrient poor, high grade metamorphic rocks (the so called Moldanubicum Zone). This is reflected in their vegetation composition, characterized by a high presence of cotton-grass (*Eriophorum vaginatum*), a species with a highly developed tolerance to low resources and a large capacity for nutrient immobilization (Cholewa and Griffith, 2004; Silvan and others, 2004). The wettest places of these SSF are covered only by *Sphagnum* mosses, followed by cotton-grass co-dominating less wet areas, while ericoids – namely blueberry (*Vaccinium myrtillus*) are co-dominant on drier hummocks. **We wanted to determine how the presence of particular vascular plant species is reflected in the peat and soil microbial characteristics, and thus to determine the possible implications of their spreading for nutrient cycling and C storage in the SSF system. Our particular hypotheses were: 1) The nonmycorrhizal cotton-grass and ericoid blueberry will differ in their tissue chemistry from the *Sphagnum* mosses, causing faster decomposition of their litter. Their presence will influence peat chemistry, enhance nutrient availability and stimulate microbial activity in comparison to the *Sphagnum*-peat. 2) There will also be differences between the vascular plant species. Cotton-grass biomass will contain more nutrients and less polyphenolic and lignin compounds than that of blueberry, which will be reflected in its lower litter C:N:P stoichiometry and higher decomposition rate. Therefore, the stimulating effect on nutrient cycling rate, microbial biomass and its activity will be more pronounced in the presence of cotton-grass than of blueberry.** To attain this, we measured and compared C, N and P contents and their stoichiometric ratios of live and senescent aboveground and belowground tissues of the studied plant species – *Sphagnum*, cotton-grass and blueberry, and in the peat, dissolved organic matter and microbial biomass taken in the patches covered only by peat moss or dominated by one of the particular plant species. The plant and peat samples were also characterized by their organic compounds composition using infrared spectroscopy. The activities of extracellular enzymes gaining C, N and P, and microbial respiration measured in peat samples, were used to assess the possible changes in peat transformation under different vegetation.

Material and methods

Study sites

The study sites are located in the Šumava Mountains, south-west Czech Republic (48°59`N, 13°28`E). Three spruce swamp forest (SSF) sites are located in the catchments of three different small brooks, situated on an upland plateau at an altitude of ca 1100 m a.s.l, with a cold and humid climate. The mean annual temperature is 4.0 °C with mean annual precipitation of 1100 mm (years 1961–1990, statistics by the Czech Hydro-Meteorological Institute). The SSF are covered by a continuous layer of *Sphagnum* mosses (dominated by *S. fallax* with the rare presence of *S. flexuosum* and *S. girgensohnii*) with wet open patches occupied by *Eriophorum vaginatum* L. (with a coverage of 25–50%) and drier microhabitats with shrubs of *Vaccinium myrtillus* L (with a coverage of 45–75%). Other plant species like *Vaccinium vitis-ideae* L., *Vaccinium oxycoccos L.*, sedges and grasses are also rarely present. The patchy distribution of the three dominants in the understory reflects variations in terrain microtopography and water level in the SSF. The tree canopy cover (*Picea abies*) varies from 0% to 80% with tree height ranging from 8 to 15 m. Total N deposition is 0.5–1 g N m^{-2} yr^{-1} (2011, statistics by the Czech Hydro-Meteorological Institute).

Aboveground and belowground plant tissue sampling and analyses

Plant samples for the purpose of this study were collected from only one of the studied sites, Tetrevska. This site was chosen due to its easy accessibility and the fact that temperature and water level dataloggers were already located there. Preliminary vegetation biomass sampling (both above and belowground) found no significant differences between the sites (Edwards, unpublished data). Since the sites are protected areas, the aim was to minimize disturbance to the sites as much as possible. The *Sphagnum* capitula, and the fully expanded sun-exposed mature leaves from the top canopy of blueberry and cotton-grass were randomly sampled (n=10) in May (beginning of the growing season), July (top season) and September (end of vegetation season) in 2013 and 2014. The senescent leaves were obtained as follows. In the case of cotton-grass, senescent leaves still attached to plants were sampled in September 2013 and in May, July and September 2014. For blueberry, recently senesced, but still attached, reddish brown leaves were sampled in September 2013 and 2014. For *Sphagnum,* the part of the stem 2-3 cm below the capitulum was considered to represent recently senescent tissue.

Belowground biomass of blueberry and cotton-grass was sampled just below the sampled plant using a soil corer (6.5 x 5.5 cm inner dimension; n=4) at the same sampling times as the aboveground plant biomass in the patches where particular plants dominated. The roots were carefully separated from the peat by hand, washed and assigned to the studied plant species. Roots from other species were discarded. The belowground samples were further separated to living and senescent tissues according to their color, structure and strength. The above and belowground plant materials were dried at 60^{o} C for 72 hours.

To address the likely differences in the quality of living and senescent biomass between *Sphagnum*, cotton-grass and blueberry, their total C and N concentrations were determined by dry combustion on an elemental analyzer (ThermoQuest, Italy). Total P was measured colorimetrically using the ammonium molybdate-ascorbic acid method on a flow injection analyzer (FIA, Lachat QC8500, Lachat Instruments, USA) after perchloric acid digestion (Kopáček and Hejzlar, 1995). Differences in N and P concentrations between live and senescent tissues of the particular plant species were used to estimate nutrient resorption efficiencies; these were calculated separately for the above- and belowground plant tissues.

The chemical composition of the plant material sampled in 2013 was assessed using infrared spectroscopy. Infrared spectra were obtained with a Bruker VERTEX 70 series FTIR (Fourier Transform InfraRed) spectrometer (Bruker Optics, Germany) equipped with a horizontal attenuated total reflectance (ATR) sampling accessory. Dried and powdered samples were inserted directly on the ATR crystal and a MIRacle high-pressure digital clamp was used to achieve even distribution and contact of the sample and crystal. Each spectrum consisted of 65 averaged absorbance measurements between 4000 and 650 cm^{-1}, with a 4 cm^{-1} resolution. Offsets in baseline and slope between the different runs (samples) were removed by standard normal variate transformation and the second derivative using the Unscrambler software (CAMO, Norway). The individual bands were assigned according to Artz et al. (2008). Summed absorbance values of the following bands were used as representative of the different organic compounds in the ordination diagrams of Fig 1: 2920 and 2850 cm^{-1} (fats, wax, lipids); 1515, 1454 and 1265 cm^{-1} (phenolics, lignin); 1550 and 1650 cm^{-1} (polypeptides); 1153, 1030 and 900 cm^{-1} (polysaccharides).

Field decomposition study

A decomposition study was conducted in the study site Tetrevska to determine whether the observed changes in the litter quality were reflected in the rate of mass loss under field conditions. Senesced leaves of cotton-grass and blueberry were collected at the end of the 2014 growing season (October) as well as roots of the two species and *Sphagnum* thalli. Subsamples of the litter material were dried at 60^o C for 48 hours and weighed to determine initial litter dry weight, while fresh litter material (1.5 g) was placed into separate litter bags (8x8cm; mesh size = 1mm). These bags were placed in the field in November 2014 with litter bags containing the leaf litter or *Sphagnum* lain on the ground within clumps of the respective species. Bags containing roots were installed in the top 15cm of the peat within clumps of the respective species using a shovel to produce a slit into which the litter bags were carefully slid so to ensure contact with the peat. Four replicate bags per each species and litter type were collected after 175 and 345 days of exposure (May and October 2015, respectively). The remaining litter was carefully removed from the mesh bags, gently washed, dried at 60^o C for 48 h and weighed.

Peat and soil solution sampling and analyses

Peat was sampled in all three SSF sites in May, July and September of 2013 and 2014 using a soil corer (6.5 x 5.5 cm inner dimension; n=4) to a depth of 30 cm in randomly selected places covered only by *Sphagnum* and in patches of cotton-grass or blueberry. The samples were homogenized by hand and roots and other woody material were removed. A portion of the soil was dried at 60^o C to constant weight, milled and analyzed for total C, N and P contents and their organic compounds composition by infrared spectroscopy as described above for plant material.

The soil solution was extracted by centrifugal-drainage at 4000 g for 1 h at 4 °C (Giesler and Lundstrom, 1993) from undisturbed peat cores, sampled from a depth of 5–15 cm from the above-defined patches with different vegetation. The extraction was done within 24 hours after peat sampling. After filtration through a low-protein-binding Express PLUS Polyethersulfone membrane (MILLGPWP) with a 0.22 µm pore size (Merck Millipore Ltd., Ireland), the soil solution was analyzed for organic C (DOC) and N (DN) concentrations on a LiquiTOC II (Elementar, Germany) while soluble reactive P (SRP), ammonium and nitrate N were analyzed colorimetrically on a flow injection analyzer (FIA Lachat QC8500, Lachat Instruments, USA).

Total soluble P was measured colorimetrically as orthophosphates on a flow injection analyzer after perchloric acid digestion (Kopáček and Hejzlar, 1995). The same solution was used to measure pH by a glass pH electrode.

Microbial biomass and activity

In fresh peat samples, microbial biomass carbon (MB-C), nitrogen (MB-N) and phosphorus (MB-P) were determined using the chloroform fumigation extraction method (Brookes and others, 1982; Brookes and others, 1985; Vance and others, 1987) within 48 hours after sampling. Samples were extracted by 0.5M potassium sulfate (1:4 w:v) in the case of MB-C and N and by 0.5M sodium bicarbonate with a pH of 8.5 (1:15 w:v) in the case of MB-P before and after chloroform fumigation for 24 hours. The dissolved organic C and dissolved N concentrations in the soil extracts were measured with a TOC/TN analyzer (LiquiTOC II, Elementar, Germany). The P content was measured spectrophotometrically at 886 nm wavelength by the ammonium molybdate-ascorbic acid method. MB-C, MB-N, and MB-P were calculated by subtracting the C, N and P concentrations in extracts from the fumigated and non-fumigated samples using correction factors of 0.3, 0.54 and 0.4, respectively.

Microbial respiration was measured as the increase of CO_2 concentration over 48 hours during incubation of fresh peat at 10°C in bottles sealed with rubber covers. Anaerobic microbial respiration was assessed similarly but the headspace of the bottles was flushed with nitrogen. CO_2 concentrations were measured on a gas chromatograph (Agilent 6850 Series, Agilent, USA).

Potential extracellular enzyme activities were determined by microplate fluorometric assays under standardized laboratory conditions. For determination of hydrolytic enzyme activities, 0.5 g of soil was suspended in 50 ml distilled water and sonicated for 4 min to disrupt the soil particles. 200 µl of the soil suspension was added to 50 µl methylumbelliferyl substrate solution for β-glucosidase (BG), phosphatase (AP) or N-acetylglucoseaminidase (NAG) determination or to 50 µl 7-aminomethyl-4-coumarin substrate solution for leucine aminopeptidase (LAP) determination (Marx et al. 2001). Plates were incubated at 20° C for 2 h. Fluorescence was quantified at an excitation wavelength of 365 nm and an emission wavelength of 450 nm using the INFINITE F200 microplate reader (TECAN, Germany). All the enzymatic activities were summed. The activity of BG represented investments into C acquisition, the sum of LAP and NAG showed N acquisition and AP was a measure of P acquisition (Sinsabaugh and others, 2009).

Statistics

The molar C:N, C:P and N:P ratios were calculated for the living and dead tissues from each of the three plant dominants, and the peat, soil microbial biomass and soil solution occurring under these dominants (Sterner and Elser, 2002). For the peat and microbial characteristics, mean values from all three sites are presented in the results, while data from individual sites are in the supplement.

Variations in plant biomass, peat, MB and soil solution characteristics among patches covered only by *Sphagnum* or with the presence of cotton-grass or blueberry were explored by principal component analysis (PCA, CANOCO 5). The measured C, N and P concentrations and their stoichiometric ratios in the samples, or infrared absorbance data, were used as response variables, while variables describing plant species and the live/dead status of the plant tissue (only for analyses of plant tissues) were passive explanatory variables. A constrained analysis (RDA) was then used to determine the proportion of data variability connected with the explanatory variables, plant species, live/dead status, site, time of sampling within the growing season (May, July, September) and sampling year (2013, 2014), from which the best predictors were then selected by interactive forward selection, with a false discovery rate used to adjust the significance of the multiple tests.

The effects of plant species on plant biomass, peat and microbial biomass characteristics were further assessed using a general linear model (with site, vegetation season and sampling year used as covariates), followed by post hoc testing with the Tukey HSD test when the effect was significant (STATISTICA 10, USA). When necessary, the data were log-transformed to meet the requirements for normalcy and variance homogeneity.

Between-species differences in decomposition rate were determined by running repeated measures ANOVAs on the relative remaining dry mass data (%) separately for each litter type. The data had normal distributions and homogeneous variances, thus no data transformations were necessary. The rate of relative mass loss for each species and litter type was determined as the slope of a linear regression (STATISTICA 10, USA).

Results

Elemental and stoichiometric characteristics of the aboveground and belowground plant tissues

Carbon content of the above- and belowground plant tissues increased in the order *Sphagnum* < cotton-grass < blueberry. The cotton-grass shoots had the highest N and P concentrations and thus the lowest C:N and C:P ratios among the studied plants (Table 1). The two other species, the living *Sphagnum* and blueberry leaves, had lower, but similar, nutrient concentrations. However, the significantly lower C concentration in *Sphagnum* resulted in its tissue C:N and C:P ratios to be markedly lower in comparison to those of the blueberry leaves. The N:P tissue ratio ranged from 19 to 23 with no significant difference among the species.

The living belowground parts, although being generally nutrient poorer than the aboveground tissues, mirrored the stoichiometric differences between both vascular plants. Cotton-grass roots were nutrient richer, with lower C:N, C:P and N:P ratios, than the belowground parts of blueberry (Table 1).

The PCA clearly separated all three plants according to the nutrient and stoichiometric characteristics of their living aboveground (pseudo-F=90.5, p=0.002, Fig. 1a) and belowground tissues (pseudo-F=17.9, p=0.002, Fig. 1c). In the first case, the differences among plant species explained 48% of the data variability (p=0.005), while this factor explained only 12% of the belowground data variability (p=0.005, results of interactive forward selection). The nutrient and stoichiometric characteristics of the plant tissues for all species changed during the season. In both years, the higher N and P concentrations in May decreased towards autumn leading to higher tissue C:N and C:P ratios in September. These temporal changes explained an additional 3-6% of the data variability (p<0.01 for both above- and belowground biomass).

The ordination diagrams further showed significant nutrient, especially P, depletion of the above- and belowground tissues after senescence, while their C concentration was not changed (Fig. 1a, c). Therefore, senescent plant parts had markedly higher C:N and C:P, and also N:P ratios than their living tissues (Table 1). The live/dead status of the tissue explained 23% of the aboveground data variability (p=0.004) and 7.3% of the belowground data variability (p=0.005). Since the sampled senescent plant material was still attached to plants, its nutrient depletion was mainly ascribed to nutrient resorption into living tissues. Generally, cotton-grass displayed the most efficient nutrient resorption with P resorption being greater than that of N. The aboveground P resorption was 65%, 52% and 41 % while N resorption was 50%, 17% and 25% for cotton-grass, blueberry and *Sphagnum*, respectively. Below ground, cotton-grass resorbed even more, 89% of P and 55% of N, while no significant nutrient resorption was found from senescent roots of blueberry. In summary, the characteristics of the aboveground senescent tissues still reflected the stoichiometric differences found among the living tissues, with cotton-grass having nutrient richer litter than blueberry. Below ground, the initially differing nutrient and stoichiometric characteristics converged in the senescent material of both vascular plants (Fig. 1c), making the senescent *Sphagnum* tissue relatively nutrient richest and senescent cotton-grass roots the most P depleted sources for microbial decomposition (Table 1).

Infrared spectra of the aboveground and belowground plant tissues

All three plant dominants differed in both their aboveground (pseudo-F=109, p=0.002, Fig. 1b) and belowground (pseudo-F=33.8, p=0.002, Fig. 1d) tissue chemical composition. The differences among plant species explained 74% of the aboveground FTIR data variability (p=0.002), while it explained only 37% of the variability for the belowground FTIR data (p=0.002). *Sphagnum* biomass had a high relative content of polysaccharides (Fig. 2a, bands at 3340, 1153, 1030 and 900 cm^{-1}) and the lowest content of aliphatic and aromatic compounds: fats, waxes, lipids (bands at 2920 and 2850 cm^{-1}), phenolic and lignin-like compounds (bands in the region 1735–1265 cm^{-1}). Cotton-grass had a similarly high content of polysaccharides as *Sphagnum*, but differed (leaves more than roots) by having a somewhat higher content of aliphatic and aromatic compounds, and polypeptides (bands at 1650 and 1550 cm^{-1}). Blueberry biomass had the highest content of aliphatic and aromatic compounds (again, leaves more than roots), and the lowest content of polysaccharides and polypeptides.

As the plant material used for IR analysis did not contain living aboveground biomass of *Sphagnum* and blueberry, we cannot document any shifts in the contents of the chemical compounds caused by senescence of these species. In the case of cotton-grass, living shoots contained more polypeptides (Fig. 2a, bands at 1650 and 1550 cm^{-1}) and a larger proportion of lignin to polysaccharides than dead ones (Fig. 1b).

The FTIR-derived characteristics of plant tissues of all species also changed during the season. However, these temporal changes explained only 1–2% of data variability. The contents of phenolic and lignin-like structures tended to increase from May to September. Polysaccharides showed the highest abundance in July and the lowest in September. Polypeptides had an opposite seasonal pattern than that of polysaccharides.

Litter decomposition of different plant species

The field data on relative mass loss were fitted by linear regression, which is relevant for the early stage of litter decomposition. Different slopes for the fitted lines pointed to significantly different litter decomposition rates of the studied species. The mass loss of aboveground litter was fastest for cotton-grass leaves, which lost 68.9 ± 14.3% of their weight during the first year of incubation in the field, while the decomposition rates for blueberry leaves (37.9 ± 3.7% y^{-1}) and *Sphagnum* (24.2 ± 8.7 % y^{-1}) were significantly lower ($p < 0.001$). Between-species differences for the roots showed the opposite result, with blueberry roots decomposing at a significantly faster rate (42.2 ± 7.6% y^{-1}) than those of cotton-grass (18.1 ± 13.4% y^{-1}, $p < 0.001$). As a result, cotton-grass roots decomposed much more slowly than its leaves, and, in fact, as slowly as the decomposition-resistant *Sphagnum* litter. The decomposition rates of blueberry leaves and roots were only slightly different.

Peat and soil solution characteristics and C:N:P stoichiometry

The presence of cotton-grass significantly lowered the N and P contents in the peat (Table 2), enhancing its C:N and C:P ratios (Fig. 1e). The nutrient depriving effect of cotton-grass was consistent at all three sites (Table S1). The cotton-grass further had a potentially acidifying effect on the peat (Table 2), which occurred on two of the three sites (Table S1). The blueberry, located on drier patches in the SSF sites (relation with soil dry mass in Fig. 1e), did not affect peat nutrient content but significantly acidified it (Table 1) at all three sites (Table S1). Generally, the total N and P contents were correlated ($r=0.418$, $p<0.05$) across all peat types. Accordingly, the peat N:P ratio remained relatively constant (Table 2). Using RDA, we were able to explain 41% of the variability in the peat characteristics, of which 28% can be ascribed to the presence of vascular plants (namely cotton-grass, 21%), 9% to the site and 4% to seasonal variations, mainly related to changes in soil water content (results of interactive forward selection).

The PCA ordination diagram for the FTIR-derived peat chemical composition separated relatively well the peats formed under particular plant species (Fig. 1f). The chemical composition of the peat formed in the presence of the two vascular plant dominants differed in a similar manner as found in their biomass. Compared to *Sphagnum* peat, the peat formed under the polysaccharide-rich cotton-grass was enriched in polysaccharides, while the peat with the contribution of blueberry was enriched in aliphatic and aromatic compounds (fats, waxes, lipids, lignin-like and phenolic compounds) (Fig. 2b). Using RDA, we were able to explain 43% of FTIR data variability, of which 38% can be ascribed to the presence of vascular plants, namely cotton-grass, and 5% to the site. Generally, our results on peat elemental and organic compounds composition show that differences in peat characteristics attributed to plant dominants are significant and larger than those caused by site differences.

In comparison to bulk peat, the soil solution contained more P, but less N, relative to C, as shown by the higher C:N but lower C:P and N:P ratios (Table 3). Similarly to the situation in the peat, each plant dominant had a specific effect also on the soil solution chemistry. The presence of blueberry in the understory enhanced the concentration of DOC (Table 3) at two of the three sites (Table S2), which indicated higher mobility and lability of soil C. Since the soluble N concentration did not change under blueberry, this soil solution had a higher C:N ratio in comparison with other plants. Overall, the content of mineral N forms in the soil solution was intermediate for blueberry peat, but the increased content of nitrates as compared to *Sphagnum* and cotton-grass peat indicated more oxic conditions (Table 3). Blueberry presence further had the potential to mobilize P, evidenced by an enhanced concentration of soluble P found at two of the three sites, and also by a higher concentration of soluble reactive P at the P richest Tetrevska site (Table S2). This ability of blueberry resulted in the systematically lowest soil solution N:P ratio for all plant dominants (Table 3). The effect of cotton-grass on the soil solution was not significant, but was coincident with its nutrient depleting effect on the bulk peat. Overall, the soil solution in the cotton-grass peat had the lowest concentration of mineral N at all three sites (Table 3 and S2). The concentrations of soluble P and soluble reactive P were lowered by cotton-grass presence only at the Tetrevska site, characterized by the highest concentrations of soluble P from the three sites (Table S2). The soil solution in patches covered only by *Sphagnum* always had the highest ammonium-N concentration indicating the highest N availability but lack of oxic conditions. In total, however, only 7% of the variability in the soil solution data can be ascribed to the dominant vegetation (RDA analysis and interactive forward selection, p=0.003), with site explaining 9%, and changes within vegetation season, mainly the increase of DOC concentration in summer (p=0.004), and inter-annual differences in the nitrate concentration in soil solution (p=0.004) (detailed data not shown) explaining 12% of data variability.

MB, its elemental stoichiometry and activity

Microbial biomass C, N and P were higher in the patches with blueberry in comparison to the other two dominants (Table 4). This blueberry effect was consistent in all three sites, although the increase in microbial C and N was not always statistically significant (Table S3). In two of the three sites, microbial P, but no other element bound in the microbial biomass, was also enhanced under cotton-grass (Table S3). The changes in microbial biomass did not significantly affect its elemental stoichiometry, although the microbial biomass under blueberry appeared to have the lowest C:P ratio, while that under cotton-grass the highest C:N ratio (Table 4). In comparison to *Sphagnum*-peat, the portion of peat N and P bound in microbial biomass was higher, exceeding 2% for N and 20% for P in the presence of both vascular plants, making microbial biomass an important nutrient pool in those types of peat. The interactive forward selection of explanatory variables showed that only 5% of the variability in the microbial biomass and its elemental stoichiometry could be ascribed to the effect of vegetation of the sampled patch, with a similar portion of variability explained by site (5%) and temporal changes in MB. A decrease in the microbial C:P and N:P ratios from May to the end of the growing season explained 5% of data variability and the year-to-year decrease in MB-N content from 2013 to 2014 explained an additional 3% (P<0.05 in all cases, detailed data not shown).

Aerobic and anaerobic microbial respiration and total enzymatic activity were comparable among the patches with different vegetation (Table 4), with the exception of the Kvilda site, where microbial respiration was higher under cotton-grass than in the other types of vegetation (Table S4). A majority of enzymatic activity (≥ 75%) was directed to P acquisition under all types of vegetation. However, in two of the sites, the portion of P-gaining enzymes was lower, while the portion of enzymes mining C was higher, in the peat formed in the presence of blueberry in comparison to both other peat types (Table S4).

Discussion

Shifts in the peatland plant community towards vascular plant dominance, driven by climate change, is predicted to have negative consequences for peatland C sink functioning (Bragazza et al. 2013; Jassey et al. 2013; Buttler et al. 2015; Dieleman et al. 2015). However, we demonstrated here that the implications on ecosystem behavior are species-specific and markedly differ between blueberry and cotton-grass, the most common vascular plants co-dominating spruce swamp forests together with *Sphagnum* spp.

Sphagnum mosses formed the N richest environment within the generally nutrient poor spruce swamp forest system

Against the general assumption that *Sphagnum* is a low quality substrate (Hájek and others, 2011; Turetsky and others, 2012), we found that *Sphagnum* biomass is rather rich in polysaccharides and nutrients. *Sphagnum*-peat, formed in the absence of any vascular plants, was also relatively nutrient rich and its soil solution contained the highest concentration of mineral (ammonium) N from the three peat types studied (Fig. 3). We suggest that the relatively high N availability in the *Sphagnum*-peat could be related to several specific characteristics of *Sphagnum* mosses: biological atmospheric N_2 fixation by cyanobacteria and methanotrophs associated with *Sphagnum* (Larmola and others, 2014), high cation exchange capacity (Verhoeven and Liefveld, 1997) and low N resorption efficiency from the senescing *Sphagnum* (only ca 25% of N was resorbed, calculated on a mass basis). Despite the highest N availability in the *Sphagnum* peat within the studied peatland, the *Sphagnum* litter decomposed very slowly in comparison to the other types of litters, and microbial biomass and activity were also low. Therefore, these microsites undoubtedly acted as C sinks. Besides the possible suppression of microbial activity by polyphenolics (e.g. Verhoeven and Liefveld, 1997) and the prevailing anaerobic conditions, another reason is that the system is also P limited. This limitation is indicated by the high peat C:P and N:P ratios in comparison to common soils (Cleveland and Liptzin, 2007) and also by the large investments into P-acquisition, which exceeded 80% of the measured activity of hydrolytic enzymes. These findings agree with the suggestion that primary production and microbial growth are P limited in peatlands (Hill and others, 2014). Therefore, environmental changes affecting P cycling and relieving P limitation of the microbial activity in the *Sphagnum* dominated peatland should be expected to impact its ability to act as a C sink.

Cotton-grass depleted nutrients from the peat and its presence did not stimulate peat decomposition in spruce swamp forests

Both above- and belowground living cotton-grass biomass were rich in polysaccharides and formed significant nutrient pools within the spruce swamp forest system. Such biomass characteristics suggest that cotton-grass presence should be connected with fast litter decomposition, the enhancement of nutrient concentrations in soil solution and acceleration of peat decomposition (Chapin, 2003 and others). However, our results did not support any of these expectations and showed that the system with cotton-grass functioned differently.

Cotton-grass appeared to be the center of a closed nutrient pool, with only small losses into the soil solution and bulk peat. The high nutrient resorption of cotton-grass, reaching 50% for N and 60–80% of P, secured effective internal N and P recycling within the plant (Fig. 3). Its large nutrient immobilization capacity can be ascribed to an effective biomass production (Tuittila and others, 1999), significant allocation of nutrients in the slowly decomposing storage organs (Silvan and others, 2004), unusual vascular system of cotton-grass enabling efficient internal nutrient recycling (Cholewa and Griffith, 2004) and the long lifespan of individual tussocks (Shaver and others, 1986). The deeply rooting system of cotton-grass facilitated nutrient uptake by the plant. The mechanisms of efficient nutrient uptake and immobilization within the plant resulted in N and P depletion from the soil solution and the formation of the nutrient poorest peat within the spruce swamp forest system (Fig. 3).

Cotton-grass is further thought to have large root exudation, which is deduced from increased CO_2 and CH_4 effluxes in its presence (Saarnio and others, 2004; Laine and others, 2012; Kuiper and others, 2014; Robroek and others, 2015b). The exudation of low molecular weight compounds commonly enhances microbial activity in the vicinity of roots and accelerates soil organic matter decomposition by the rhizosphere priming effect (Kuzyakov, 2002). We found that cotton-grass presence enhanced the proportions of total peat N and P bound in the soil microbial biomass in comparison to the *Sphagnum*-peat, which documented high efficiency of the plant-microbe relations in the mining of nutrients from the peat and in their subsequent immobilization. However, we did not find any significant increase either in soil microbial biomass or its exoenzymatic activity, which could be a sign of increased peat decomposition in the presence of cotton-grass. Still, the fact that cotton-grass enriched the peat with easily decomposable compounds can be deduced from enhanced microbial respiration under aerobic conditions, as found in one of the three studied sites. In anaerobic conditions, however, this cotton-grass effect disappeared. Lack of the expected stimulation effect of cotton-grass might be explained by strong nutrient limitation of microbial activity, because of the nutrient depletion by cotton grass, as well as the prevailing anoxic conditions, which disable the functioning of oxidative enzymes and lower the energetic gain of microbial metabolism.

The decomposition rate of the polysaccharide rich but nutrient poor cotton-grass root litter was very low under such conditions, being similar to that of the decay-resistant *Sphagnum* litter (Hájek and others, 2011). This seems to be a general phenomenon since decomposition of cotton-grass root litter was markedly slower in comparison to other root litter types (*Carex* sp., *Betula nana*, fine roots of *Pinus sylvestris*) as found in a field study in boreal peatlands (Straková and others, 2012). Well recognizable residues of its dead organs can be found even in peat layers formed thousands of years ago (Kalnina and others, 2015). As a result, a combination of high primary productivity and slow tissue decomposition makes cotton-grass a typical peat-forming species with C sink function (Tuittila and others, 1999; Silvan and others, 2004; Kivimaki and others, 2008).

Based on these results, we suggest that cotton-grass presence does not relieve the microbial community from nutrient limitation and supports the peatland C sink function. Supportive data about its efficient C and nutrient economics enable us to expect that cotton-grass will have a similar effect on peat chemistry over a wide range of peatlands in which it can be typically found, including nutrient-poor open bogs and pine bogs, boreal peatlands, cut-away and also restored peatlands.

Blueberry promoted soil organic matter decomposition by significantly enhancing P availability

As hypothesized, blueberry biomass and attributes varied from that of both other plant species. Noteworthy, blueberry was the nutrient poorest plant dominant but still it was not efficient in the internal recycling of nutrients within its biomass (Fig. 3). It resorbed only 17% of N and ca 52% of P from senescing leaves and almost no nutrients from its dying belowground biomass. The lower need for a closed nutrient cycling within blueberry biomass could be due to nutrient income via ericoid mycorrhizal symbionts, which are able to mobilize N and P complexed in recalcitrant organic matter and facilitate their plant uptake (Cairney and Meharg, 2003; Read and others, 2004).

The more open nutrient cycling within blueberry biomass increased P availability, resulting in the highest concentrations of P in the soil solution among all three plant species (Fig. 3). In relation to this, microorganisms decreased their costs expended on P gaining but invested more into enzymes acting in C acquisition. Ericoid mycorrhizae associated with blueberry roots can play an important role in extracellular enzyme production and increased P availability (Read, 1996; Read and others, 2004). Enhanced concentration of nitrate-N in the soil solution and its decreasing pH indicated more oxic conditions in the peat under blueberry. The blueberry litter, although rather nutrient poor and rich in aliphatic and aromatic compounds, thus decomposed relatively faster. The increasing amount of dissolved organic C in the soil solution supported the assumption about faster decomposition.

The higher nutrient availability and presence of ericoid mycorrhizae were mirrored in the microbial biomass, which was larger than in the other peat types and had lower C:N:P stoichiometry (Fig. 3). Therefore, the microbial biomass under blueberry represented an important sink/source of nutrients with relatively fast turnover in the range of days to weeks (Schmidt and others, 2007). This made the nutrient cycling under blueberry more dynamic with the nutrients released during microbial turnover more accessible to plant uptake.

In summary, the blueberry tissues represented a less concentrated but, thanks to the large biomass, still significant nutrient stock within the spruce swamp forest, similar to the cotton-grass biomass. However, contrary to cotton-grass, the blueberry nutrient pool seemed to be more open, with larger losses of N and P to the peat, which could reduce nutrient limitation of the microbial decomposers and potentially stimulate peat decomposition. Our results thus support the projection of others (Bragazza and others, 2013; Bragazza and others, 2015) that the spreading of ericoid shrubs in peatlands would enhance organic matter decomposition and increase nutrient cycling, with negative implications for C sequestration.

Conclusions

Vascular plant cover in peatlands will likely increase with climate change (Elmendorf and others, 2012). Previous studies demonstrated that this spreading can feed back to change microbial activity in the peat (Bragazza and others, 2015; Robroek and others, 2015b). Our data showed that the potential effect of vascular plants on peat properties, and soil microbial biomass and activity is species-specific and need not necessarily result in increased organic matter decomposition.

The presence of blueberry enhanced the availability of the limiting nutrient P, connected with an increase in soil microbial biomass and the activities of C acquiring enzymes. Its spreading in peatlands, which could occur with lower water levels and the formation of an oxic upper peat layer, thus may result in increased organic matter decomposition, which would negatively affect the capacity of peatlands to act as C sinks, as proposed by others (Bragazza and others, 2013; Bragazza and others, 2015).

Differently, the potential spread of cotton-grass can occur in nutrient-poorer peatlands with increasing temperatures but stable water levels (Wahren and others, 2005; Salmon and others, 2016). Cotton-grass is thought to provide large amounts of easily degradable compounds to the soil microbial community. However, at the same time, it has a high capacity to immobilize nutrients and strongly depletes P and N from the peat, which is further reflected in the C:N:P stoichiometry of the microbial biomass. The harsh conditions and prevailing anoxia in the upper peat layer retard the decomposition of cotton-grass litter and result in no significant enhancement in microbial biomass and exoenzymatic activity. Therefore, the spread of cotton-grass would not change or may even enhance the functioning of peatlands as C sinks.

Acknowledgements:

This study was supported by the Grant Agency of Czech Republic (13-17398S), the Ministry of Youth Sports and Education of Czech Republic (LM2015075) and the Academy of Finland (No. 1259190, for PS). We thank Terezia Říhová for analyses on FIA, Ville Narhi for elemental analyses, Dan Vaněk for analyses on LiquiTOC and Ondřej Žampach for his help with the field work and FTIR measurements.

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Table 1. Plant tissue chemistry. Average concentrations of C, N and P (%), and their molar stoichiometric ratios in the aboveground and belowground plant tissues of *Sphagnum*, cotton-grass and blueberry, either living or senescent (still attached to plant). Plant material was sampled in May, June and September 2013 and 2014 in the site Tetrevska. (Mean, standard deviation of mean SEM, n=60). Capital letters refer to significant differences in particular characteristics between live and senescent tissues, while lower case letters show differences among plant species (results of One-way ANOVAs and post hoc comparisons, p<0.05).

Plant biomass		Sphagnum			Cotton-grass			Blueberry		
Aboveground biomass										
live	C (%)	41.2^{aA}	±	0.1	46.5^{bA}	±	0.1	48.7^{cA}	±	0.1
	N (%)	1.00^{bA}	±	0.03	2.15^{cA}	±	0.05	0.77^{aA}	±	0.03
	P (%)	0.09^{aA}	±	0.00	0.26^{bA}	±	0.01	0.08^{aA}	±	0.00
	C:N	48.7^{bA}	±	1.3	26.3^{aA}	±	0.8	78.6^{cA}	±	2.9
	C:P	1157^{bA}	±	36	501^{aA}	±	20	1641^{cA}	±	65
	N:P	23.4^{bA}	±	0.8	19.0^{aA}	±	0.4	21.1^{aA}	±	0.6
senescent	C (%)	42.0^{aA}	±	0.3	46.7^{bA}	±	0.1	49.2^{cA}	±	0.1
	N (%)	0.76^{aB}	±	0.03	1.09^{bB}	±	0.04	0.64^{aB}	±	0.04
	P (%)	0.06^{bB}	±	0.00	0.09^{cB}	±	0.01	0.04^{aB}	±	0.00
	C:N	64.2^{bB}	±	2.1	52.6^{aB}	±	2.0	96.2^{cB}	±	5.2
	C:P	1925^{bB}	±	75	1440^{aB}	±	86	3225^{cB}	±	202
	N:P	32.5^{bB}	±	1.2	26.9^{aB}	±	0.7	34.3^{bB}	±	1.8
Belowground biomass										
live	C (%)				45.7^{aA}	±	0.7	49.6^{bA}	±	0.2
	N (%)				1.46^{bA}	±	0.17	0.56^{aA}	±	0.02
	P (%)				0.27^{bA}	±	0.03	0.05^{aA}	±	0.00
	C:N				51.2^{aA}	±	10.1	114.2^{bA}	±	4.2
	C:P				580^{aA}	±	81	3324^{bA}	±	209
	N:P				13.7^{aA}	±	1.0	30.2^{bA}	±	1.6
senescent	C (%)				47.4^{aB}	±	0.1	49.4^{bA}	±	0.1
	N (%)				0.67^{aB}	±	0.02	0.71^{aB}	±	0.03
	P (%)				0.03^{aB}	±	0.00	0.05^{aA}	±	0.00
	C:N				88.2^{aB}	±	2.8	93.5^{aB}	±	4.0
	C:P				4784^{bB}	±	271	4227^{aA}	±	380
	N:P				52.8^{aB}	±	2.2	43.0^{aB}	±	2.6

Table 2. Peat chemistry. Average concentrations of C, N and P (%), their molar stoichiometric ratios and pH of the peat formed in patches covered only by *Sphagnum* or affected by the presence of cotton-grass or blueberry. Peat cores were sampled in May, June and September 2013 and 2014 in three spruce swamp forest sites. (Mean, standard deviation of mean SEM, n=72). Results of GLM on the effect of plant dominants are shown, with site and sampling time as covariates. Lower case letters show differences among peat characteristics formed in the presence of different plant dominants (p<0.05).

	Sphagnum			Cotton-grass			Blueberry			Plant	Site	Time
Ctot	43.8^{a}	±	0.9	45.1^{a}	±	0.2	46.8^{a}	±	0.3	ns	***	ns
Ntot	1.63^{b}	±	0.05	1.12^{a}	±	0.05	1.59^{b}	±	0.03	***	**	ns
Ptot	0.09^{b}	±	0.00	0.05^{a}	±	0.00	0.08^{b}	±	0.00	***	ns	ns
C:N	25.0^{a}	±	0.6	44.3^{b}	±	1.8	29.2^{a}	±	0.8	***	ns	ns
C:P	1457^{a}	±	132	2226^{b}	±	71	1609^{a}	±	69	***	**	ns
N:P	44.0^{a}	±	2.6	46.0^{a}	±	1.5	46.1^{a}	±	1.5	ns	***	ns
pH	4.31^{a}	±	0.04	4.01^{a}	±	0.03	3.94^{b}	±	0.02	***	***	**

ns	nonsignificant
*	p<0.05
**	p<0.01
***	p<0.001

Table 3. Soil solution chemistry. Average concentrations of dissolved organic C (DOC; mg l^{-1}), soluble N (SN; mg l^{-1}) and P (SP; µg l^{-1}), their molar stoichiometric ratios, concentrations of mineral N forms (N-NH4, N-NO3; mg l^{-1}) and soluble reactive P (SRP, µg l^{-1}) in the soil solution extracted from peat cores from patches covered by *Sphagnum* and affected by the presence of cotton-grass or blueberry. Peat cores were sampled in May, June and September 2013 and 2014 in the three spruce swamp forest sites. (Mean, standard deviation of mean SEM, n=72). Results of GLM on the effect of plant dominants are shown, with site and sampling time as covariates. Lower case letters show differences among solution characteristics in the presence of different plant dominants (p<0.05).

	Sphagnum	Cotton-grass	Blueberry	Plant	Site	Time
DOC	66.5^{a} ± 5.5	72.9^{a} ± 5.2	92.3^{b} ± 6.8	**	**	***
SN	1.92^{a} ± 0.15	1.59^{a} ± 0.10	1.78^{a} ± 0.14	ns	***	ns
SP	0.28^{a} ± 0.04	0.23^{a} ± 0.02	0.51^{b} ± 0.12	*	***	ns
C:N	51.3^{a} ± 4.6	67.4^{ab} ± 6.2	77.8^{b} ± 7.8	**	ns	***
C:P	889^{a} ± 72	1124^{a} ± 106	927^{a} ± 76	*	***	***
N:P	21.5^{b} ± 1.5	20.6^{b} ± 1.7	14.9^{a} ± 1.1	**	*	***
NH_4	0.59^{c} ± 0.06	0.15^{a} ± 0.01	0.26^{b} ± 0.03	***	***	***
NO_3	0.09^{a} ± 0.01	0.10^{a} ± 0.01	0.17^{b} ± 0.03	**	ns	*
SRP	0.17^{a} ± 0.03	0.11^{a} ± 0.01	0.27^{a} ± 0.09	ns	***	ns

ns	nonsignificant
*	p<0.05
**	p<0.01
***	p<0.001

Table 4. Microbial biomass C, N and P (MB-C, MB-N, MB-P; $\mu g\ g^{-1}$) and their molar stoichiometric ratios, proportions of peat C, N, and P bound in the microbial biomass (%), microbial respiration in aerobic and anaerobic conditions ($\mu l\ CO_2\ g^{-1}\ h^{-1}$) and the sum of hydrolytic enzymatic activity and proportions of C, N and P-gaining enzymatic activities in the peat formed in patches covered only by *Sphagnum* or affected by the presence of cotton-grass or blueberry. Peat cores were sampled in May, June and September 2013 and 2014 in the three spruce swamp forest sites. (Mean, standard deviation of mean SEM, n=72). Results of GLM on the effect of plant dominants are shown, with site and sampling time as covariates. Lower case letters show differences among peat characteristics formed in the presence of different plant dominants.

	Sphagnum			Cotton-grass			Blueberry			Plant	Site	Time
MB-C	3217^{a}	±	321	3613^{ab}	±	240	4354^{b}	±	336	*	***	ns
MB-N	276.2^{a}	±	25.1	301.3^{a}	±	31.3	459.0^{b}	±	39.4	***	**	ns
MB-P	123.3^{a}	±	9.7	150.1^{a}	±	12.4	201.6^{b}	±	14.4	***	ns	**
C:N	17.35^{a}	±	1.77	24.24^{b}	±	4.67	15.34^{a}	±	1.58	*	*	**
C:P	90.15^{a}	±	15.34	97.82^{a}	±	19.07	68.4^{a}	±	6.39	ns	**	**
N:P	9.23^{a}	±	2.36	6.41^{a}	±	0.95	6.23^{a}	±	0.63	ns	**	**
MB-C/Ctot	0.75^{a}	±	0.08	0.82^{a}	±	0.05	0.94^{a}	±	0.07	ns	***	*
MB-N/Ntot	1.42^{a}	±	0.15	2.12^{b}	±	0.22	2.26^{b}	±	0.19	***	***	ns
MB-P/Ptot	15.07^{a}	±	1.63	27.62^{b}	±	2.37	26.51^{b}	±	2.05	***	ns	***
Microbial respiration aerobic	7.78^{b}	±	0.48	8.31^{b}	±	0.44	6.02^{a}	±	0.32	**	***	*
Microbial resp. anaerobic	1.32^{a}	±	0.13	1.35^{a}	±	0.13	1.17^{a}	±	0.09	ns	ns	***
Sum of enzymatic activity	933.1	±	83.6	754.1	±	49.9	866.5	±	72.0	ns	**	*
% C gaining enzymes	14.5^{a}	±	1.0	12.8^{a}	±	0.7	18.1^{b}	±	1.4	**	ns	ns
% N gaining enzymes	2.5^{a}	±	0.3	3.6^{a}	±	0.3	3.5^{a}	±	0.4	*	***	ns
% P gaining enzymes	83.0^{b}	±	1.2	83.6^{b}	±	0.9	78.5^{a}	±	1.5	**	*	ns

ns	nonsignificant
*	p<0.05
**	p<0.01
***	p<0.001

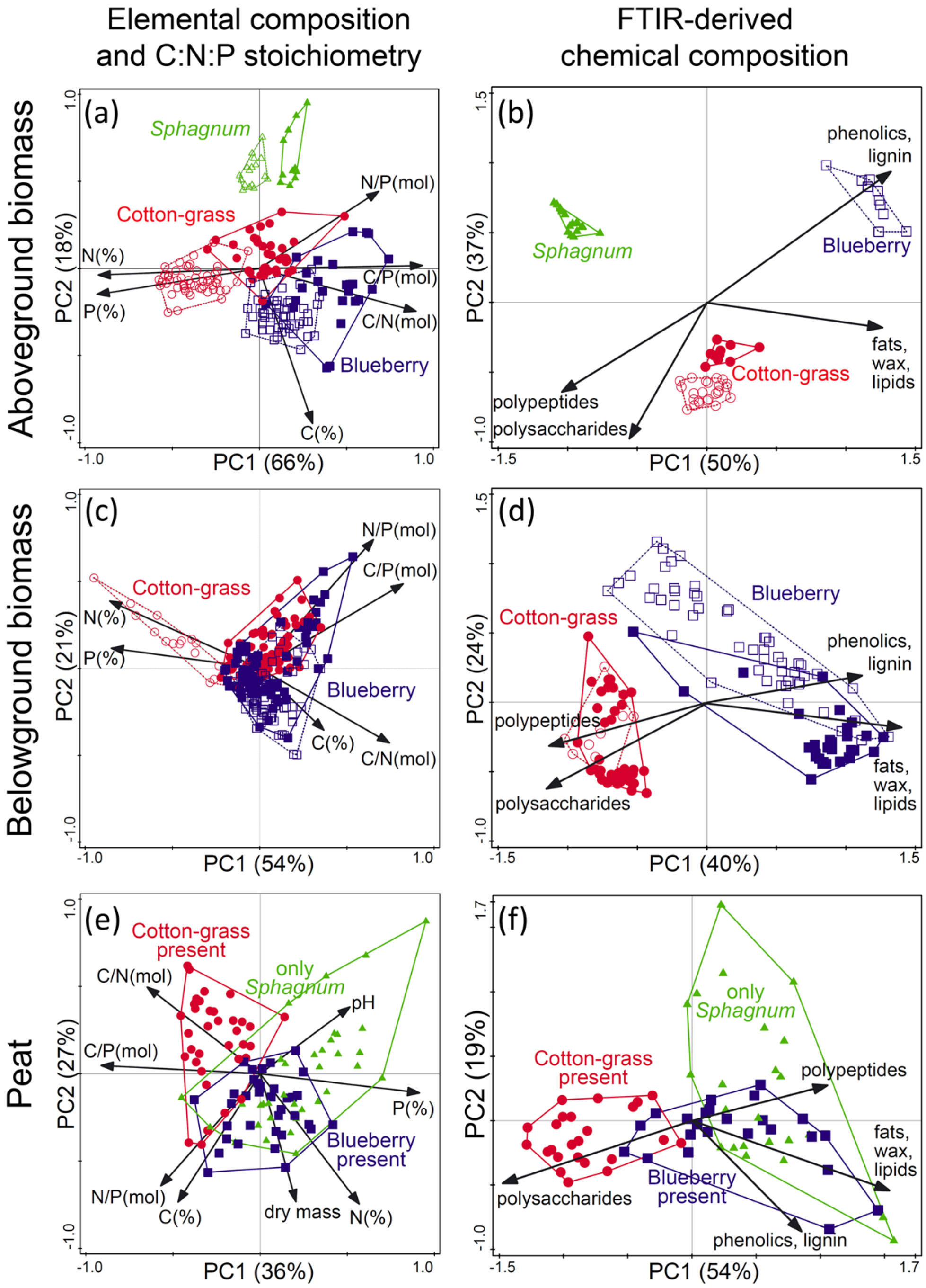

Fig. 1. Plant tissue and peat chemistry: Ordination diagrams from principal component analysis (PCA) showing the relations between tissue elemental concentrations and the stoichiometry of *Sphagnum*, cotton-grass and blueberry, and FTIR derived chemical composition for their (a, b) aboveground and (c, d) belowground biomass, divided into living (open symbols) and senescent (full symbols) tissue, and for (e, f) peat formed in their presence. While graphs a-d are based on plant data from the Tetrevska site only, the graphs e-f show peat data from all three studied sites.

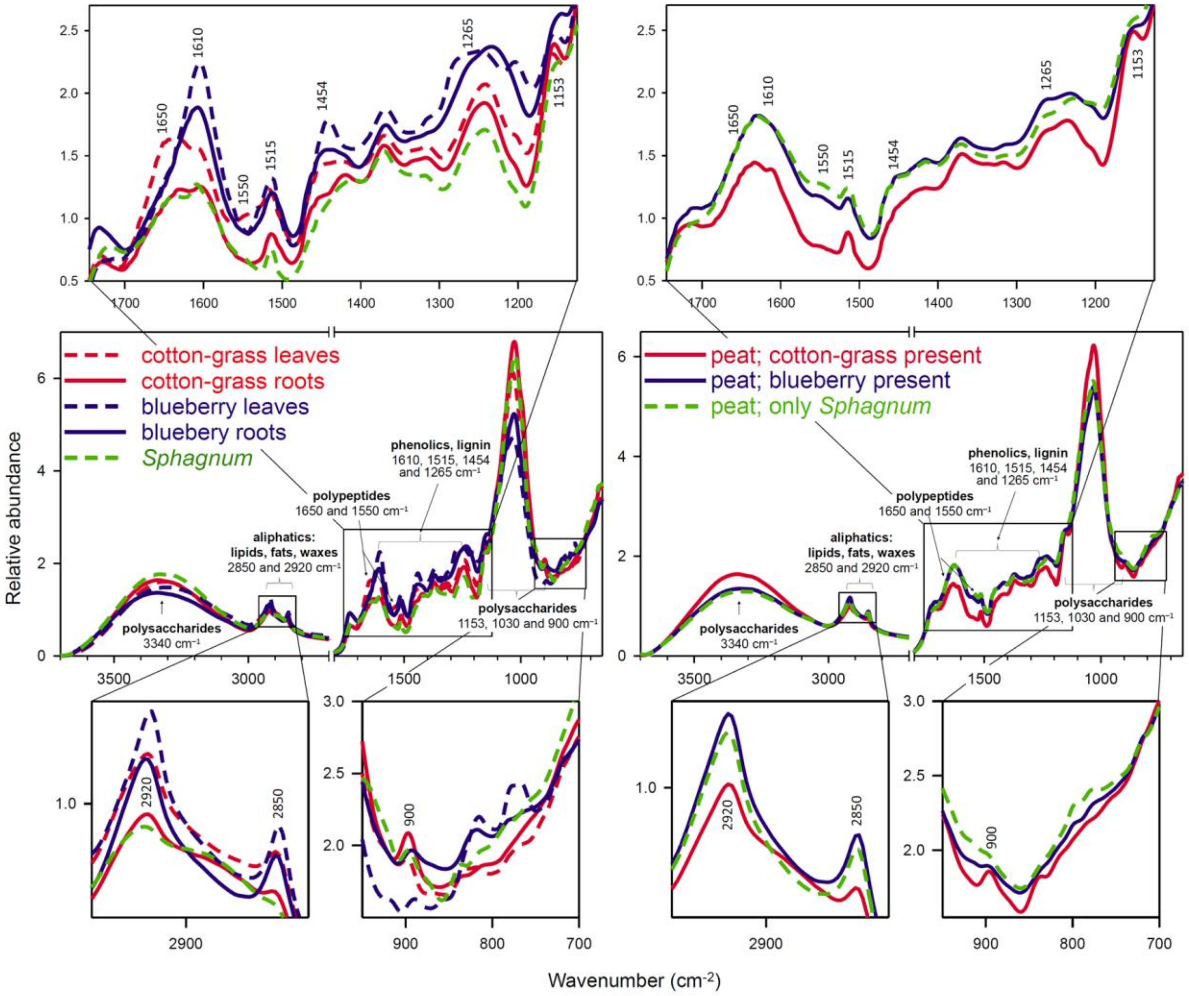

Fig. 2. Infrared spectra of (a) leaves and roots of cotton-grass and blueberry, and *Sphagnum* capitula and (b) peat formed in the prevalence of particular plants, with detailed views of the parts of the spectra showing significant differences among plant tissues. Band assignments as according to Artz et al. 2008.

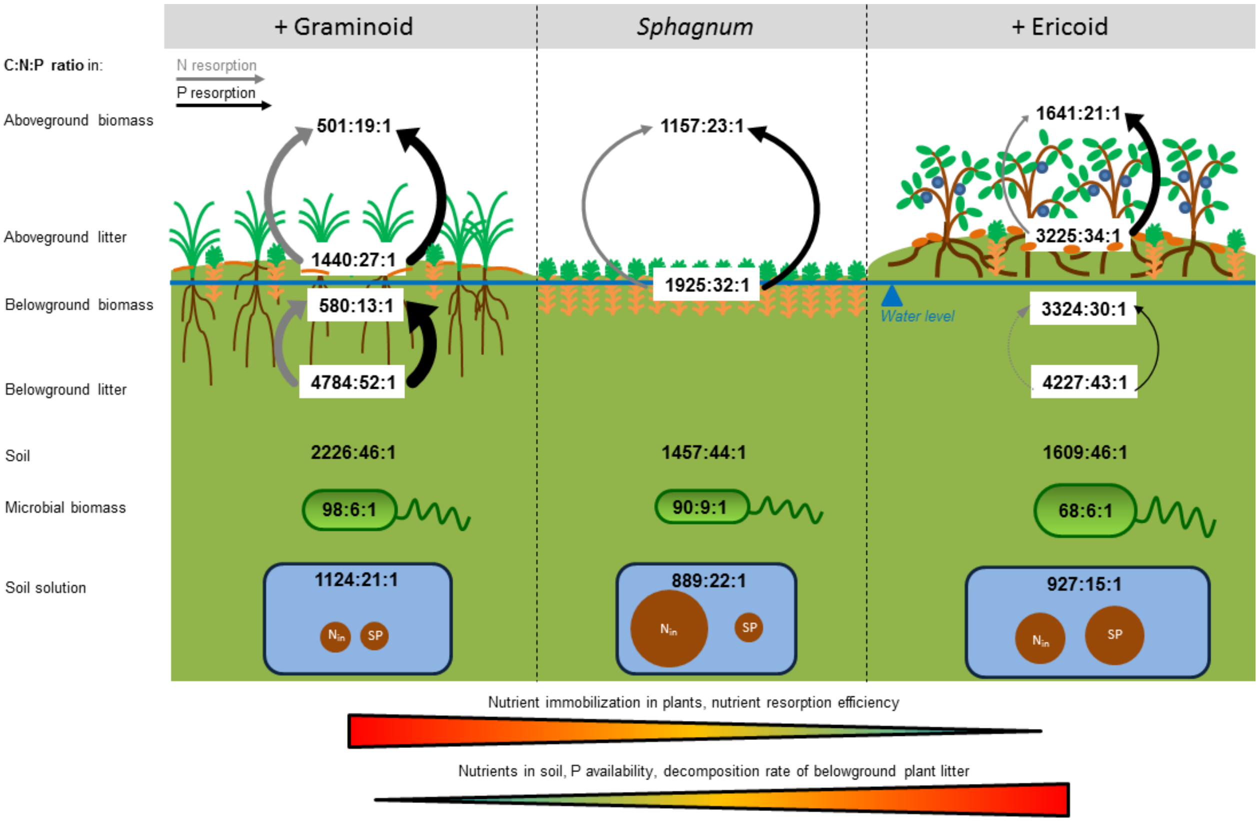

Fig. 3. Schema of the functioning of the spruce swamp forest system in the presence of the studied plant dominants; with *Sphagnum* only (in the center), in the presence of cotton-grass (on the left) and blueberry (on the right). The C:N:P stoichiometry of the living and senescent biomass of particular plant dominant is shown, their nutrient resorption efficiencies are indicated by the width of the arrows. Belowground, the C:N:P stoichiometry of the peat, microbial biomass and soil solution formed in the presence of particular plant dominant is shown, based on average data from the three study sites. Sizes of ovals and circles show the relative differences in the microbial biomass, soil organic C pool and concentration of mineral N and soluble phosphorus among the areas affected by different plant dominants. The figure demonstrates the decreasing concentration of nutrients in the living plant tissues but also decreasing nutrient efficiencies from cotton-grass over *Sphagnum* to blueberry. At the same time, P availability increased in the soil, which was connected with enhanced microbial biomass and the decomposition rate of belowground plant litter in the same direction.