UNIVERSITY OF HELSINKI

https://helda.helsinki.fi

Boreal bog plant communities along a water table gradient differ in their standing biomass but not their biomass production

Korrensalo, Aino; Kettunen, Laura; Laiho, Raija; Alekseychik, Pavel; Vesala, Timo ...

2018-03

John Wiley and Sons Inc.

http://hdl.handle.net/10138/325829

Korrensalo, A, Kettunen, L, Laiho, R, Alekseychik, P, Vesala, T, Mammarella, I & Tuittila, E-S 2018, 'Boreal bog plant communities along a water table gradient differ in their standing biomass but not their biomass production', Journal of Vegetation Science, vol. 29, no. 2, pp. 136-146. https://doi.org/10.1111/jvs.12602

Downloaded from Helda, University of Helsinki institutional repository. https://helda.helsinki.fi

This is an electronic reprint of the original article.

This reprint may differ from the original in pagination and typographic detail.

Please cite the original version.

MS. AINO KORRENSALO (Orcid ID : 0000-0002-0320-8689)

Accepted Article

Article type : Research article

Co-ordinating Editor : Stephen Roxburgh

Coordinating Editor: Dr. Stephen Roxburgh

Boreal bog plant communities along a water-table gradient differ by their standing biomass but not by their biomass production

Aino Korrensalo[*]*, Laura Kettunen, Raija Laiho, Pavel Alekseychik, Timo Vesala, Ivan Mammarella & Eeva-Stiina Tuittila*

Aino Korrensalo (aino.korrensalo@uef.fi)[1]

Laura Kettunen (laurk@student.uef.fi)[1]

Raija Laiho (raija.laiho@luke.fi)[2]

Pavel Alekseychik (pavel.alekseychik@helsinki.fi)[3]

Timo Vesala (timo.vesala@helsinki.fi)[3,4]

Ivan Mammarella (ivan.mammarella@helsinki.fi)[3]

Eeva-Stiina Tuittila (eeva-stiina.tuittila@uef.fi)[1]

[1]School of Forest Sciences, University of Eastern Finland, P.O. BOX 111, FI-80101 Joensuu, Finland

[2]Natural Resources Institute Finland, FI-00790 Helsinki, Finland

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/jvs.12602
This article is protected by copyright. All rights reserved.

[3]Department of Physics, University of Helsinki, P.O. BOX 684, FI-00014 Helsinki, Finland

[4]Department of Forest Sciences, University of Helsinki, P.O. BOX 27, FI-00014 Helsinki, Finland

[*]Corresponding author: aino.korrensalo@uef.fi

Accepted Article

Abstract

Question: Peatlands are a globally important carbon storage due to the imbalance between plant biomass production and decomposition. Distribution of live standing biomass (BM, dry mass g m^{-2}) and biomass production (BMP, dry mass g m^{-2} growing $season^{-1}$) are both known to be dependent on water table (WT). However, the the relations of BM and BMP to WT variation are poorly known. Here we investigated, how the above- and belowground BM and BMP of three different plant functional types (PFTs); dwarf-shrubs, sedges and *Sphagnum* mosses relate to natural WT variation within an ombrotrophic boreal bog. In addition, we estimated the ecosystem-level BMP and compared that with the ecosystem net primary production (NPP) derived from eddy covariance (EC) measurements.

Location: Siikaneva bog, Ruovesi, Finland

Methods: We quantified above- and belowground BM and BMP of PFTs along the WT gradient, divided into six plant community types. Plant community scale BM and BMP were upscaled to the ecosystem level. NPP was derived from EC measurements using a literature-based ratio of heterotrophic respiration to total ecosystem respiration.

Results: BM varied from 211 to 979 g/m² among the plant community types, decreasing gradually from dry to wet community types. In contrast, BMP was similar between the plant community types (162-216 g/m²), except on nearly vegetation-free bare peat surfaces where it

This article is protected by copyright. All rights reserved.

was low (38 g/m²). Vascular plant BM turnover rate (BMP:BM, year^{-1}) varied from 0.14 to 0.30 among the plant community types being the highest in sedge-dominated hollows. On average 56 % of the vascular BM was produced belowground. Mosses, when present, produced on average 31 % of the total BM, ranging from 16 to 53% depending on the community type. EC-derived NPP was higher than measured BMP due to underestimation of certain components.

Conclusions: We found out that the diversity of PFTs decreases the spatial variability in productivity of a boreal bog ecosystem. The observed even distribution of BMP resulted from different WT optima and BMP:BM of dwarf-shrubs, sedges and *Sphagnum* species. These differences in biomass turnover rate and species responses to environmental conditions may provide a resiliency mechanism for bog ecosystems in changing conditions.

Keywords: aboveground biomass; biomass turnover; dwarf-shrub; functional diversity; peatland; plant functional type; root biomass; sedge; microtopography; *Sphagnum*.

Nomenclature: Hämet-Ahti et al. (1998) for vascular plants; Laine et al., (2009) for mosses.

Abbreviations: BM (live standing biomass), BMP (biomass production), BMP:BM (biomass turnover rate), NPP (net primary production), EC (eddy covariance), WT (water table from the peat surface)

Introduction

Peatlands produce more organic material than can be decomposed due to subsurface anoxia resulting from prevailing waterlogged conditions. For this reason, these ecosystems are an important carbon sink storing up to one third of the soil carbon globally as partly decomposed plant matter, peat (Gorham 1991; Yu et al. 2012). Ombrotrophic boreal bogs typically have

This article is protected by copyright. All rights reserved.

Accepted Article

high spatial variation in water table (WT) depth, which has a strong positive correlation with live standing biomass (BM, dry mass g m^{-2}) (Laine et al. 2012). Future changes in climate may lower the WT of boreal peatlands resulting in a possible shift towards predominance of woody vegetation (Laine et al. 1995; Laiho et al. 2003; Strack et al. 2006). Such a shift is likely to affect also the temporal and spatial patterns of BM and biomass production (BMP dry mass g m^{-2} a^{-1}), which is the input component of the peatland carbon sink.

Vegetation changes induced by WT drawdown emerge as altered dominance of existing plant communities (Laiho et al. 2003; Strack et al. 2006), which in bogs range compositionally from solely low sedge -dominated to predominantly dwarf-shrubs (Rydin and Jeglum 2013). These components of the plant community, as well as the *Sphagnum* mosses typical of bogs, show varying WT optima where their aboveground BM or BMP is the largest (e.g. Laine et al. 2012). Thorough understanding of variation in BM and BMP over natural WT gradients found in bogs could thus help predict the response of boreal bogs to climate change. Notwithstanding the numerous studies concerning the distribution of peatland BM and BMP, we found only one that included all BM components of different plant communities along the WT gradient of one bog site (Vasander et al. 1982). Therefore, there is clearly need for additional, direct field measurements of BM and BMP that include both above- and belowground components of vascular plants as well as mosses.

Dwarf-shrubs can form up to 70 % of the total aboveground BM of ombrotrophic bogs (Bubier et al. 2006), and both their BM and BMP decrease monotonically with rising WT (Wallén 1987; Laine et al. 2012). In comparison to dwarf-shrubs, sedges have generally higher WT optima for aboveground BM and BMP (Vasander et al. 1982; Wallén et al. 1987), are more efficient photosynthesizers relative to their photosynthetic area (Leppälä et al. 2008) and have higher BM turnover rate (BMP:BM ratio, y^{-1}) (Forrest, 1971; Shaver and Chapin, 1991). Belowground, root BMP has been found to increase with decreasing WT,

This article is protected by copyright. All rights reserved.

Accepted Article

as the oxic peat layer becomes deeper (Murphy & Moore 2010; Weltzin et al. 2000). Dwarf-shrubs produce most of their root BM in the uppermost 20 cm and sedges and herbs in the deeper peat layers (Murphy et al. 2009b). Up to 90 % of vascular plant BMP may occur belowground (Saarinen 1996) in peatlands, but the relation of BM with WT is known mainly for aboveground components. Although the BMP:BM ratio is likely to vary within a bog site, as the abundances of sedges and dwarf-shrubs vary over the WT gradient, many former studies are limited to standing BM only, and data on BMP are much more limited (e.g. Bubier et al. 2006; Murphy et al. 2009a; Laine et al. 2012).

Sphagnum mosses, covering up to 100 % of the surface of ombrotrophic bogs, are the most important peat-forming group in boreal bog ecosystems (Gunnarsson 2005) with BMP of 132-278 g m^{-2} a^{-1} (Tint 1982; Vasander 1982; Moore et al. 2002; Kosykh et al. 2008). *Sphagna* can be seen to seasonally balance out the productivity of vascular plants; they are especially important for the ecosystem-level carbon sink strength in early spring and late autumn when the vascular leaf area is low (Moore et al. 2006). Contrary to vascular plants, *Sphagnum* BM and BMP are the highest at WTs close to peat surface (Vasander 1982; Wallén 1987, Welzin et al. 2001; Gunnarsson 2005; Bubier et al. 2006), because the species typical of wet habitats are more efficient BM producers than the hummock species (Gunnarsson 2005). The role of *Sphagna* in total BMP may thus vary along the WT gradient; however, this has received little specific attention so far.

Our aim was to quantify the variation in BM and BMP in relation to WT gradient in an ombrotrophic boreal bog with heterogeneous surface topography formed by the varying plant communities. We aimed to quantify all BM components, i.e., BM and BMP of above- and belowground parts of vascular plants as well as *Sphagnum* mosses, in six plant community types. To validate our measurements, we estimated the BM and BMP also at the ecosystem level and compared them with earlier studies. The ecosystem-level BMP estimate

This article is protected by copyright. All rights reserved.

Accepted Article

was also compared with the net primary production (NPP) estimate derived from eddy covariance (EC) measurements using a literature-based ratio of autotrophic and heterotrophic respiration.

We hypothesize that i) BM and BMP decrease with WT closer to the peat surface and ii) the BMP:BM ratios differ among plant community types along the WT gradient.

Materials and methods

Study site and sampling design

The study site is an ombrotrophic bog (61°50' N, 24°12' E), a part of the Siikaneva peatland complex in Ruovesi, Western Finland in the Southern Boreal vegetation zone (Ahti et al. 1968). The average annual temperature sum in the area (base temperature 5 °C) is 1318 degree-days, average annual rainfall is 707 mm, and the average annual, January and July temperatures are 4.2, -7.2 and 17.1 °C, respectively (averages of the 30-year-period 1982-2011 from Juupajoki-Hyytiälä weather station). Except for a few stunted individual Scots pines (*Pinus sylvestris*), the site is treeless and the ground vegetation consists of a mosaic of plant communities where species composition varies with WT (Table 1). An EC flux tower is located in the center of the site, and the study area is defined as a 30 meter radius circle around the tower.

After exploring the variation in vegetation along the WT gradient we divided the site into seven plant community types ranging from dry high hummocks to ponds (Table 1). The open water surfaces without vegetation were excluded from the BM study. We established 18 sample plots, sized 56 x 56 cm around the EC tower in three groups of six plots, visually selected to represent the six different plant community types. To record the

This article is protected by copyright. All rights reserved.

Accepted Article

WT variation throughout the growing season for each community type, we measured weekly the WT depth from perforated plastic tubes installed next to each sample plot.

To quantify the nutrient concentrations of surface peat along the WT gradient, we took 18 surface peat samples of 3 x 3 x 20 cm close to the sample plots, three from each of the six community types. The three samples were pooled together, dried at 40 °C and milled. The mass-based concentration (% of peat dry mass) of P was measured using plasma mass spectrometer (ICP-OES, IRIS Intrepid ll XSP), and those of C and N using elemental analyzer (Vario Max Cube, Elementar, Germany). The nutrient concentrations of the surface peat in each plant community are reported in Table 1.

Measuring aboveground vascular live standing biomass and biomass production

The seasonal development of leaf area index (LAI, m^2 m^{-2}) (Wilson et al. 2007) was used to estimate the BM and BMP of the vascular plants. For this, we set up five 8 x 8 cm subplots inside each of the 18 sample plots. We counted the number of green leaves from the subplots 11 times over the growing season 2014 (April 4 – Sept 9 of 2014). Average green area per leaf or per stem-cm was measured with a scanner on each LAI measurement day. The LAI of each species was then calculated for each sample plot and measurement day, based on the number of leaves inside the subplots and the average leaf size.

Aboveground BM of the vascular plants was estimated by converting the growing season LAI maxima of each species at each of the 18 sample plots into BM (g m^{-2}). For this, linear regressions were established for each species between LAI and BM, including green leaves, stems and branches (linear parameters and a more detailed description of the method are provided in Appendix 1). Aboveground vascular BMP was estimated by converting the change in LAI between the spring minimum and mid-summer maximum to dry mass (g m^{-2}) (Appendix 1); this was done for each species at each of the 18 sample plots.

This article is protected by copyright. All rights reserved.

Accepted Article

Measuring belowground live standing biomass and biomass production

Belowground BM was measured in August 2015 from 18 peat cores of 3 x 3 x 50 cm taken close to the sample plots from similar plant communities. The cores were cut into 10 cm layers. Peat was washed out of roots with water and dead roots (based on visual estimation) were removed. Living roots, including rhizomes and coarse roots, were divided into dwarf-shrub and sedge roots, which were then dried at 40 °C for 48 h before weighing.

Belowground BMP was estimated with the root ingrowth core method described in Laiho et al. 2014. Cylinder-shaped mesh bags filled with live-root-free *Sphagnum* peat were installed into each of the 18 sample plots in October 2012 and removed in October 2014. In the laboratory, the cores were cut into 10 cm layers and washed, classified, dried and weighed similarly to the belowground BM samples. The sum of live and dead roots in the cores was divided by two to obtain an annual BMP estimate (see Bhuiyan et al. 2016), as the bags were in place for two years.

Measuring Sphagnum moss live standing biomass and biomass production

BM of *Sphagnum* mosses at each of the 18 sample plots was defined for each species by converting their visually estimated projection cover (m^2 m^{-2}) to dry mass of capitula (g m^{-2}) using the conversion factors in Appendix 1.

To define the biomass increment of each *Sphagnum* species we used the cranked wire method (Clymo 1970). We installed 66 wires into as homogenous as possible patches of each of the eight species to be measured. The length growth, the shoot density and the weight of one centimeter of stem were defined in each of the 66 patches between May 19 and September 7 of 2014. Using these values, the BMP in dry mass g m^{-2} growing $season^{-1}$ was calculated for each of the cranked wire patches (Appendix 2). For each species, we calculated the species-wise average length growth and BMP estimates by averaging results of

This article is protected by copyright. All rights reserved.

Accepted Article

species-specific patches (Appendix 2). BM production of each *Sphagnum* species in each sample plot was calculated using these species-wise averages multiplied by the relative cover of each species inside the plots (m^{-2} m^2) by the BMP (g m^{-2} growing $season^{-1}$) of the species.

Statistical analysis

We tested the differences between the six plant community types of 22 standing biomass and biomass production components using linear mixed-effects models. More detailed information about the statistical tests and pairwise comparisons between the community types is given in Appendix 3. The differences in root BM and BMP among peat layers were tested with a one-way ANOVA test for each community type separately. Statistical analysis were done using R-software (version 3.2.0, www.r-project.org). Linear mixed effects models were fitted using the lme function from the nlme package in R.

Upscaling to the ecosystem level

To define the cover of both the six plant community types and each plant species within the study site, we conducted a systematic vegetation inventory in June 2013 within 30 m from the EC tower. This was identified as an area where 60% of the EC flux is coming from in unstable conditions based on footprint calculations with the Kormann and Meixner (2001) model. We estimated the projection cover of each species and defined the community types in 121 circular plots, sized 0.071 m^2, which were arranged as a regular grid around the EC tower. Community cover (% of total area) from this inventory was multiplied by BM and BMP averages of the permanent sample plots for each of the seven plant community types (six with BM estimates). The weighted values of each community type were then summed to give ecosystem-level values of standing BM and BMP. We also calculated error estimates for the ecosystem-level BM and BMP estimates by weighting the standard errors of the community-type means by the areal covers of each community type.

This article is protected by copyright. All rights reserved.

Accepted Article

Ecosystem level net primary production (NPP) estimate

To have an independent comparison for our ecosystem-level BMP estimate, we derived an NPP estimate from NEE measured by the EC tower at the site. The raw EC data was recorded at a 2.4 m high mast with a METEK-USA1 anemometer and a LI-7200 CO_2/H_2O gas analyzer. NEE was calculated from the raw EC data following standard routines of processing (EddyUH software, Mammarella et al. 2016) and quality control.

Ecosystem respiration (R_e) model values were calculated from a Q_{10}-type relationship between peat temperature at 5 cm depth and nocturnal CO_2 flux:

$$R_e = R_{ref} Q_{10}^{\left(\frac{T_p - T_{ref}}{10}\right)} \quad \text{(Eq. 1)}$$

where T_p is the peat temperature at a 5cm depth (˚C), T_{ref} the reference temperature (12˚C), R_{ref} the reference respiration (123 mg(CO_2) m^{-2} h^{-1}), and the temperature sensitivity Q_{10} is 3.49.

Heterotrophic respiration (R_h) was estimated using the proportion of R_h from R_e derived from literature, falling within the range of 43-65% (Crow and Wieder, 2005). Using the lower and upper limit of this range, the range of ecosystem-level NPP was estimated as NPP = NEE – R_h.

Results

Total live standing biomass and biomass production

In agreement with our first hypothesis, total BM (*Sphagna* and above- and belowground components of vascular plants summed up) was highest in dry vegetation communities and decreased steadily towards communities with higher WT (Fig. 1a). As a result, BM was the largest (979.3 ± 52.5 g m^{-2}, mean ± S.E. from here on) in high hummocks and the lowest (211.2 ± 81.8 g m^{-2}) in bare peat surfaces (Fig. 1a, Appendix 4). However, against the

This article is protected by copyright. All rights reserved.

Accepted Article

hypothesis, total BMP was rather even among the plant community types along the WT gradient (Fig. 2a). The modest decrease in total BMP with increasing WT was not statistically significant. Only the sparsely vegetated bare peat surfaces had lower BMP than the other community types (Fig. 2a, Appendix 5e). This balanced pattern was a result of offsetting responses of the studied PFTs to WT (Appendix 6a-b).

Standing biomass and biomass production of different plant functional types

Both BM and BMP of dwarf-shrubs, above- as well as belowground, were greatest at high hummocks and decreased sharply towards the wet end of the WT gradient (Figs. 1e and 2e, Appendix 4c and 5c). The response of total BM to WT was largely shaped by this negative WT response of above- and belowground dwarf-shrub BM (Appendix 6a-c). This was due to dwarf-shrubs having a larger BM than the other PFTs combined in four out of six community types (Appendix 4c). Dwarf-shrub belowground BMP was the largest in the top 0-10 cm layer and declined towards the deeper layers in the three dwarf-shrub-dominated community types (Appendix 7d).

Unlike the distribution of overall standing BM and shrub BM, sedge BM was concentrated on the wet end of the WT gradient both above- and belowground (Fig. 1e, Appendix 4c). However, the effect of WT on total sedge BM was much weaker in comparison to dwarf-shrubs (Fig. 1e and 1f). Belowground sedge BM did not significantly differ between the plant community types (Fig. 1f) or peat layers (Appendix 7b). Aboveground, the only difference was that sedge BM in high hummocks and hummocks was lower than in high lawns and hollows (Fig. 1f). Similarly to sedge BM, sedge BMP tended to increase with WT (Appendix 6d and 6e) being highest (81.1 ± 5.7 g m^{-2} growing $season^{-1}$) in hollows and lowest in high hummocks (18.5 ± 5.8 g m^{-2} growing $season^{-1}$) (Fig. 2f, Appendix 5c). Sedge belowground production only showed a relation to peat depth in hollows, where

This article is protected by copyright. All rights reserved.

Accepted Article

the highest amount of root production was found in the topmost 0-10 cm, because shallow-rooted *R. alba* was dominant (Appendix 7e).

Sphagnum mosses had the highest capitulum BM in hummocks (141.2 ± 5.1 g m^{-2}) and high lawns (146.2 ± 4.4 g m^{-2}) (Appendix 4d, Figs. 1c), i.e. at intermediate WTs (Appendix 6c). *Sphagnum* BMP optimum seemed to occur at higher WTs than their BM optimum (Appendix 6c and 6f). *Sphagnum* BMP was highest in lawns at WT of -4 cm below the moss surface (Fig. 2c, Table 1,). Here, BMP of *Sphagna* was 91.2 ± 8.0 g m^{-2} growing $season^{-1}$ and the greatest number of species was found (Appendix 5d).

Biomass turnover rate

Both above- and belowground, dwarf-shrubs had lower BMP to BM ratio (BMP:BM) than sedges (Fig. 3a). *Sphagnum* BMP:BM increased with habitat wetness; hummock species had the lowest BMP:BM and hollow species the highest (Fig. 3b). The BMP:BM of vascular plants was higher above- than belowground (Fig. 3a). The differences between dwarf-shrubs and sedges in this sense remained masked by the very high variation in belowground sedge BM (Appendix 5b).

Ecosystem level standing BM, BM production and NPP

Total BM within 30 m radius from the EC tower, calculated as a weighted average of the community types, was 587 ± 119 g m^{-2}, the majority of which, 446 ± 118 g m^{-2}, was root BM. Vascular aboveground BM was 59 ± 10 g m^{-2} and *Sphagnum* capitulum BM 82 ± 4 g m^{-2} (Table 2).

Total BMP for the same area was 132 ± 15 g m^2 growing $season^{-1}$, which was more evenly distributed between BM components than standing BM. During the growing season, the BMP of aboveground of vascular plant components was 44 ± 7 g m^{-2}, roots 47 ± 8 g m^{-2}, and *Sphagna* 41 ± 6 g m^{-2} (Table 2).

This article is protected by copyright. All rights reserved.

Accepted Article

The growing season (May 1 – Sept 30, 2014) NPP estimate derived from EC measurements at the study site ranged from 166 to 202 g CO_2-C m^{-2}. Since carbon content of the organic material in the almost undecomposed surface peat was found to be between 44 and 72 % (Table 1), our BMP estimate converted to carbon falls between 58-95 g C m^2 growing $season^{-1}$, which is considerably lower than the NPP estimate.

Discussion

Both above- and belowground BM decreased towards the wet end of the WT gradient, which supported our hypothesis and was in line with earlier studies (e.g. Vasander 1982; Moore et al. 2002; Murphy & Moore 2010; Laine et al. 2012). The dwarf-shrub BM concentrated in the driest plant community types could not be offset by sedges having their largest BM at high and *Sphagna* at intermediate WTs. BMP of these PFTs showed similar responses to WT variation as BM, again in agreement with earlier studies (Vasander 1982, Gunnarsson 2005). However, contrary to our hypothesis and some earlier research (Kosykh et al. 2008), the total BMP of the studied bog did not show a decrease in relation to WT. A similar even pattern has been observed in some earlier studies considering only aboveground BMP (Tint 1982; Moore et al. 2002). Only bare peat surfaces had lower BMP than other plant community types, which all were similar in terms of BMP. Thus, unlike BM, the increase in the BMP of the other PFTs compensated for the decrease in BMP of the shrubs.

The different patterns of BM and BMP reflect the higher BMP:BM of sedges and hollow *Sphagna* in relation to dwarf-shrubs and hummock *Sphagna* (Fig. 3). *Sphagnum* species growing in wet habitats are known to have a higher photosynthesis rate than hummock species (Gunnarsson 2005; Korrensalo et al. 2016). In our study, this was demonstrated well by the shift in WT optimum between BM (-13 cm) and BMP (-5 cm) of *Sphagna* (Fig. 1). Also, sedges are known to have a higher photosynthesis rate in relation to

This article is protected by copyright. All rights reserved.

Accepted Article

their BM than dwarf-shrubs (Leppälä et al. 2008). The difference in BM turnover rate between the hummock and hollow species reflects their different ecological strategies in relation to resources, mainly water and nutrients, which were earlier described as fast and slow strategies (Reich 2014). In wet hollows, where water availability rarely limits the growth, sedges have a shorter leaf life span, higher specific leaf area and higher BM turnover rate than shrubs dominating the dry hummocks, where low water availability favors slow-growing plants that use the same leaf tissue for a longer time. Unlike vascular plants, *Sphagna* do not have roots to access water, so the difference in resource use strategy may be even more pronounced among them. Also, in large forest datasets, the species with short leaf life spans have been found to have lower BM and higher BMP:BM; interestingly, total BMP does not seem to be correlated with leaf life span, a trend also seen in our study (Reich et al. 1992). However, more studies are needed to reveal the role of nutrients in addition to water in the even BMP along the WT gradient.

The large diversity of vegetation at our site is linked to the large microtopographical variation present, which is characteristic of some bogs (Sottocornola et al. 2009). In addition to the WT variation itself, this diversity is suggested to be partly a result of resource contrast between the plant communities at the opposite ends of the WT gradient (Belyea 2007). Resource contrast is the result of nutrients being washed from hummocks to wetter surfaces in areas of high precipitation, and conversely, nutrients accumulating on hummocks when evapotranspiration is high (Eppinga et al. 2010). If the ratio between evapotranspiration and precipitation is to change in the future, the processes driving the bog patterning may also change with yet unknown consequences for the binding of carbon into plant biomass.

Both BM and BMP estimates obtained in this study were mostly lower than previously reported for peatlands, even for similar, treeless, nutrient poor ombrotrophic bogs

This article is protected by copyright. All rights reserved.

Accepted Article

(aboveground BMP in Tint 1982). However, many of the earlier estimates have been measured at drier bog sites with a higher cover of arboreal vegetation (Vasander 1982; Moore et al. 2002) or with higher nutrient status (Kosykh et al. 2008) than in this study. In hollows, at WTs similar to high hummocks of our study, Moore et al. (2002) found an aboveground BM estimate of 308 g m^{-2}, which is reasonably close to the 247.3 ± 24.8 g m^{-2} estimate at our high hummocks. Moreover, we only measured BM of *Sphagnum* capitula because of the large uncertainty related to separating dead and live sections of *Sphagnum* stems (Clymo 1970).

However, it seems that our BMP estimate is somewhat underestimated, as it was notably smaller than the NPP estimate derived from EC measurements. Also the NPP estimate contains some error sources, e.g. the possibility of a systematic overestimation in EC-derived R_e (Phillips et al. 2016). However, both the NPP estimate and the mean annual NEE fell within the range of previously studied boreal and temperate bogs (Vasander 1982; Tint 1982; Petrescu et al. 2015; Wilson et al. 2016; Pavel Alekseychik, unpublished data). The explanation for the gap between the NPP and BMP estimates is presumably threefold. First, some components of BMP may have been underestimated in this study. The vertically installed root ingrowth cores may not have been able to capture all of the vertically growing sedge fine roots, and the installation of the cores may have caused disturbance, possibly leading to underestimation of root BMP. *Sphagnum* BMP may have been underestimated by not measuring their growth in early spring and late autumn. Second, there are some components of BMP that the methods used in this study were not able to capture. These include e.g. root production in >50 cm of depth, vascular plant reproductive tissues, coarse roots, rhizomes and the few sporadic trees at our site. Third, the discrepancy between our BMP and NPP estimates may not only be due to BMP underestimation, as it is known that a part of annual NPP does not accumulate as plant BM. Instead, it is lost via e.g. leached root

This article is protected by copyright. All rights reserved.

Accepted Article

exudates, volatile organic compounds (VOCs), litterfall during the growing season and herbivory (Clark et al. 2001; Roxburgh et al. 2005). A possible explanation beyond these three points is that *Sphagna* are known to uptake a large part of their C as CO_2 and CH_4 coming from peat decomposition below (Smolders et al. 2001; Limpens et al. 2008; Larmola et al. 2010), but how this affects the ecosystem-level C fluxes is not yet known. The contribution of most of the components underestimated or missing in this study remain poorly known for peatlands. Therefore, the discrepancy between the two estimates highlights the difficulties in empirically estimating BMP and NPP. Based on these results, it seems essential to continue empirical work in quantifying the missing components of NPP to fully understand the carbon sink of peatland ecosystems.

The effect of changing climatic conditions on the carbon binding function of peatlands has been studied both empirically (Weltzin et al. 2000; Breeuwer et al. 2009) and using process-based models (Frolking et al. 2010; Heijmans et al. 2013; Gong et al. 2013). Due to the previously observed increase in standing BM and BMP with decreasing WT, many studies predict an increase of bog BM production both above- and belowground and a shift towards larger dominance of woody vegetation resulting from water level drawdown (Laine et al. 1995; Breeuwer et al. 2009; Holmgren et al. 2015). The lower decomposability of shrubs and *Sphagna* associated with drier habitats is significant for the carbon binding function of bogs (Turetsky et al. 2008; Straková et al. 2011). In the bog site studied here, paleoecological data has revealed that past shifts towards a drier climate have increased the abundance of drier habitats (Mathijssen et al. 2016). However, current climate scenarios for the boreal vegetation zone (IPCC 2013) do not seem to predict a drop in WT sufficient to induce a shift from current vegetation of Siikaneva to that of previously studied sites, e.g. dwarf-shrub dominance in Moore et al. (2002) or higher tree cover as in Vasander (1982). Instead, temperature and precipitation fluctuations have been predicted to increase in the near

This article is protected by copyright. All rights reserved.

Accepted Article

future (IPCC 2013). In model simulations, the bog vegetation of temperate climate zone was observed to be rather resilient towards changes in WT, but changes in temperature were more likely to shift the vegetation towards dominance of trees (Heijmans et al. 2013).

The even BMP across the WT gradient observed in this study may be a mechanism for resiliency towards climate-induced WT fluctuations, because of the different WT optima of the species present. In a previous study by Breeuwer et al. (2009), decreased and fluctuating WT did not result in a significant decrease of aboveground vegetation cover and BM of a bog, exactly due to the diversified responses of dwarf-shrubs, sedges and *Sphagnum* species to changed WT. Our results suggest that in a bog with diverse PFTs having differing WT optima, the BMP may not change dramatically after a small and fluctuating WT drawdown. This, again, could provide stability for the ecosystem carbon sink under changing moisture regimes. In addition to WT, the abundances of bog plants are known to have differential responses to changing temperatures among species, or even within one species depending on its habitat (Buttler et al. 2015). In addition to long-term changes in climate, also the annual weather conditions are likely to change the contributions of different plant communities and plant species to ecosystem-scale BMP reported here during one growing season. In order to reveal how the net primary productivity of bog ecosystems responds to moisture and temperature variations and what the role of PFTs is in this process, more long-term studies are needed - either experimental studies or comparisons of sites with different PFT composition over several years. In addition, paleoecological studies may offer insight to the longer-term changes in peatland vegetation patterning in response to larger shifts in climatic conditions.

This article is protected by copyright. All rights reserved.

Accepted Article

Accepted Article

Acknowledgements

The work presented here is supported by the Faculty of Science and Forestry in the University of Eastern Finland, the Finnish Cultural Foundation, the Academy of Finland (287039, 118780, 1284701, 1282842, 286190), Academy professor projects (282842 and 284701), ICOS-Finland (281255), MONIMET LIFE12 ENV/FI/409 and Centre of Excellence 307331. We would also like to thank the staff at Hyytiälä Forest Research Station and Salli Uljas, Janne Sormunen, María Gutierrez, Laura Kettunen, Eva-Stina Kerner and Antonio Cestelo for their help with the measurements and Nicola Kokkonen for revising the English language of the manuscript.

References

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5: 169-211.

Belyea, L.R. 2007. Climatic and topographic limits to the abundance of bog pools. *Hydrological Processes* 21: 675–687.

Bhuiyan, R., Minkkinen, K., Helmisaari, H.-S., Ojanen, P., Penttilä, T., & Laiho, R. 2016. Estimating fine-root production by tree species and understorey functional groups in two contrasting peatland forests. *Plant and Soil*. doi: 10.1007/s11104-016-3070-3

Breeuwer, A., Robroek, B.J.M., Limpens, J., Heijmans, M.M.P.D., Schouten, M.G.C., & Berendse, F. 2009. Decreased summer water table depth affects peatland vegetation. *Basic and Applied Ecology* 10: 330–339.

Bubier, J., Crill, P., Mosedale, A., Frolking, S., & Linder, E. 2003. Peatland responses to varying interannual moisture conditions as measured by automatic CO_2 chambers. *Global Biogeochemical Cycles* 17(2): 1066.

This article is protected by copyright. All rights reserved.

Accepted Article

Bubier, J.L., Moore, T.R., & Crosby, G. 2006. Fine-scale vegetation distribution in a cool temperate peatland. *Canadian Journal of Botany* 84: 910–923.

Buttler, A., Robroek, B.J., Laggoun-Défarge, F., Jassey, V.E., Pochelon, C., Bernard, G., Delarue, F., Gogo, S., Mariotte, P., Mitchell, E.A., Bragazza, L. 2015. Experimental warming interacts with soil moisture to discriminate plant responses in an ombrotrophic peatland. *Journal of Vegetation Science* 26(5):964-74.

Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J. 2001. Measuring net primary production in forests: concepts and field methods. *Ecological Applications* 11: 356–370.

Clymo, R.S. 1970. The Growth of Sphagnum: Methods of Measurement. *The Journal of Ecology* 58: 13.

Crow, S. E. & Wieder, R. K. 2005. Sources of CO_2 emission from a northern peatland: Root respiration, exudation and decomposition. *Ecology* 86: 1825–1834. doi:10.1890/04-1575

Eppinga, M.B., Rietkerk, M., Belyea, L.R., Nilsson, M.B., Ruiter, P.C.D., & Wassen, M.J. 2010. Resource contrast in patterned peatlands increases along a climatic gradient. *Ecology* 91: 2344–2355.

Forrest, G.I. 1971. Structure and Production of North Pennine Blanket Bog Vegetation. *The Journal of Ecology* 59: 453.

Frolking, S., Roulet, N.T., Tuittila, E., Bubier, J.L., Quillet, A., Talbot, J., & Richard, P.J.H. 2010. A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation. *Earth System Dynamics* 1: 1–21.

This article is protected by copyright. All rights reserved.

Accepted Article

Gong, J., Kellomäki, S., Wang, K., Zhang, C., Shurpali, N., & Martikainen, P.J. 2013. Modeling CO2 and CH4 flux changes in pristine peatlands of Finland under changing climate conditions. *Ecological Modelling* 263: 64–80.

Gorham, E. 1991. Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. *Ecological Applications* 1: 182.

Gunnarsson, U. 2005. Global patterns of *Sphagnum* productivity. *Journal of Bryology* 27: 269–279.

Heijmans, M.M.P.D., van der Knaap, Y.A.M., Holmgren, M., & Limpens, J. 2013. Persistent versus transient tree encroachment of temperate peat bogs: effects of climate warming and drought events. *Global Change Biology* 19: 2240–2250.

Holmgren, M., Lin, C.-Y., Murillo, J.E., Nieuwenhuis, A., Penninkhof, J., Sanders, N., van Bart, T., van Veen, H., Vasander, H., Vollebregt, M.E., & Limpens, J. 2015. Positive shrub-tree interactions facilitate woody encroachment in boreal peatlands (R. Bardgett, Ed.). *Journal of Ecology* 103: 58–66.

Hämet-Ahti, L., Suominen, J., Ulvinen, T. & Uotila, P. (eds.) 1998. *Retkeilykasvio (Field Flora of Finland)*, Ed. 4. Finnish Museum of Natural History, Helsinki.

IPCC, 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., & Midgley, P.M., (Eds.)]. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 1535 pp, doi:10.1017/CBO9781107415324

Kormann, R., & Meixner, F.X. 2001. An analytical footprint model for non-neutral stratification. *Boundary-Layer Meteorology* 99: 207–224.

This article is protected by copyright. All rights reserved.

Korrensalo, A., Hájek, T., Vesala, T., Mehtätalo, L., & Tuittila, E.-S. 2016. Variation in photosynthetic properties among bog plants. *Botany* 94: 1127–1139.

Kosykh, N.P., Koronatova, N.G., Naumova, N.B., & Titlyanova, A.A. 2008. Above- and below-ground phytomass and net primary production in boreal mire ecosystems of Western Siberia. *Wetlands Ecology and Management* 16: 139–153.

Laiho, R., Vasander, H., Penttilä, T., & Laine, J. 2003. Dynamics of plant-mediated organic matter and nutrient cycling following water-level drawdown in boreal peatlands: Plant-mediated OM and nutrient cycling. *Global Biogeochemical Cycles* 17(2): 1053.

Laiho, R., Bhuiyan, R., Straková, P., Mäkiranta, P., Badorek, T., & Penttilä, T. 2014. Modified ingrowth core method plus infrared calibration models for estimating fine root production in peatlands. *Plant and Soil* 385: 311–327.

Laine, J., Vasander, H., & Laiho, R. 1995. Long-Term Effects of Water Level Drawdown on the Vegetation of Drained Pine Mires in Southern Finland. *Journal of Applied Ecology* 32(4): 785–802. doi:10.2307/2404818

Laine, J., Harju, P., Timonen, T., Laine, A., Tuittila, E.-S., Minkkinen, K., Vasander, H. 2009. *The Intricate Beauty of Sphagnum Mosses - a Finnish Guide to Identification*. University of Helsinki, Department of Forest Ecology.

Laine, A.M., Bubier, J., Riutta, T., Nilsson, M.B., Moore, T.R., Vasander, H., & Tuittila, E.-S. 2012. Abundance and composition of plant biomass as potential controls for mire net ecosytem CO_2 exchange. *Botany* 90: 63–74.

Larmola, T., Tuittila, E-S., Tiirola, M., Nykänen, H., Martikainen, P.J., Yrjälä, K., Tuomivirta, T., Fritze, H. 2010. The role of Sphagnum mosses in the methane cycling of a boreal mire. *Ecology* 91: 2356–2365.

This article is protected by copyright. All rights reserved.

Accepted Article

Accepted Article

Leppälä, M., Kukko-Oja, K., Laine, J., & Tuittila, E.-S. 2008. Seasonal dynamics of CO_2 exchange during primary succession of boreal mires as controlled by phenology of plants. *Ecoscience* 15: 460–471.

Limpens, J., Berendse, F., Blodau, C., Canadell, J.G., Freeman, C., Holden, J., Roulet, N., Rydin, H. akan, & Schaepman-Strub, G. 2008. Peatlands and the carbon cycle: from local processes to global implications–a synthesis. *Biogeosciences* 5: 1475–1491.

Mammarella, I., Peltola, O., Nordbo, A., Järvi, L., & Rannik, Ü. 2016. Quantifying the uncertainty of eddy covariance fluxes due to the use of different software packages and combinations of processing steps in two contrasting ecosystems. *Atmospheric Measurement Techniques*, 9: 4915-4933.

Mathijssen, P.J.H., Väliranta, M., Korrensalo, A., Alekseychik, P., Vesala, T., Rinne, J., & Tuittila, E.-S. 2016. Reconstruction of Holocene carbon dynamics in a large boreal peatland complex, southern Finland. *Quaternary Science Reviews* 142: 1–15.

Moore, T.R., Bubier, J.L., Frolking, S.E., Lafleur, P.M., & Roulet, N.T. 2002. Plant biomass and production and CO2 exchange in an ombrotrophic bog. *Journal of Ecology* 90: 25–36.

Moore, T.R., Lafleur, P.M., Poon, D.M.I., Heumann, B.W., Seaquist, J.W., & Roulet, N.T. 2006. Spring photosynthesis in a cool temperate bog. *Global Change Biology* 12: 2323–2335.

Murphy, M.T., McKinley, A., & Moore, T.R. 2009a. Variations in above- and below-ground vascular plant biomass and water table on a temperate ombrotrophic peatland. *Botany* 87: 845–853.

Murphy, M., Laiho, R., & Moore, T.R. 2009b. Effects of Water Table Drawdown on Root Production and Aboveground Biomass in a Boreal Bog. *Ecosystems* 12: 1268–1282.

This article is protected by copyright. All rights reserved.

Accepted Article

Murphy, M.T., & Moore, T.R. 2010. Linking root production to aboveground plant characteristics and water table in a temperate bog. *Plant and Soil* 336: 219–231.

Petrescu, A.M.R., Lohila, A., Tuovinen, J.-P., Baldocchi, D.D., Desai, A.R., Roulet, N.T., Vesala, T., Dolman, A.J., Oechel, W.C., (…) & Cescatti, A. 2015. The uncertain climate footprint of wetlands under human pressure. *Proceedings of the National Academy of Sciences* 112: 4594–4599.

Phillips, C.L., Bond-Lamberty, B., Desai, A.R., Lavoie, M., Risk, D., Tang, J., Todd-Brown, K., & Vargas, R. 2016. The value of soil respiration measurements for interpreting and modeling terrestrial carbon cycling. *Plant and Soil*. doi: 10.1007/s11104-016-3084-x

Reich, P.B. 2014. The world-wide "fast-slow" plant economics spectrum: a traits manifesto (H. Cornelissen, Ed.). *Journal of Ecology* 102: 275–301.

Reich, P.B., Walters, M.B., & Ellsworth, D.S. 1992. Leaf Life-Span in Relation to Leaf, Plant, and Stand Characteristics among Diverse Ecosystems. *Ecological Monographs* 62: 365–392.

Roxburgh, S.H., Berry, S.L., Buckley, T.N., Barnes, B., Roderick, M.L. 2005. What is NPP? Inconsistent accounting of respiratory fluxes in the definition of net primary production. *Functional Ecology* 19: 378–382.

Rydin, H., & Jeglum, J.K. 2013. *The Biology of Peatlands*. OUP Oxford.

Saarinen, T. 1996. Biomass and production of two vascular plants in a boreal mesotrophic fen. *Canadian Journal of Botany* 74: 934–938.

Shaver, G.R., & Chapin, F.S. 1991. Production: Biomass Relationships and Element Cycling in Contrasting Arctic Vegetation Types. *Ecological Monographs* 61: 1–31.

This article is protected by copyright. All rights reserved.

Smolders, A.J.P., Tomassen, H.B.M., Pijnappel, H.W., Lamers, L.P.M., & Roelofs, J.G.M. 2001. Substrate-derived CO2 is important in the development of Sphagnum spp. *New Phytologist* 152: 325–332.

Sottocornola M., Laine M., Kiely G., Byrne K.A. & Tuittila E-S. 2009. Vegetation and environmental variation in an Atlantic blanket bog in South-western Ireland. *Plant Ecology* 203: 69–81. doi: 10.1007/s11258-008-9510-2

Strack, M., Waddington, J.M., Rochefort, L., & Tuittila, E.-S. 2006. Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown: Water table and peatland CO2 exchange. *Journal of Geophysical Research: Biogeosciences* 111: n/a-n/a.

Straková, P., Niemi, R.M., Freeman, C., Peltoniemi, K., Toberman, H., Heiskanen, I., Fritze, H., & Laiho, R. 2011. Litter type affects the activity of aerobic decomposers in a boreal peatland more than site nutrient and water table regimes. *Biogeosciences* 8: 2741–2755.

Tint, R. 1982. On the productivity of treeless bog communities. In: Masing, V. (Ed.) *Peatland ecosystems*: 93-101. Valgus, Tallinn.

Turetsky, M.R., Crow, S.E., Evans, R.J., Vitt, D.H., & Wieder, R.K. 2008. Trade-offs in resource allocation among moss species control decomposition in boreal peatlands. *Journal of Ecology* 96: 1297–1305.

Vasander, H. 1982. Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. *Annales Botanici Fennici* 19: 103–125.

Wallén, B. 1987. Growth pattern and distribution of biomass of Calluna vulgaris on an ombrotrophic peat bog. *Holarctic Ecology* 10: 73–79.

This article is protected by copyright. All rights reserved.

Accepted Article

Weltzin, J.F., Pastor, J., Harth, C., Bridgham, S.D., Updegraff, K., & Chapin, C.T. 2000. Response of bog and fen plant communities to warming and water-table manipulations. *Ecology* 81: 3464–3478.

Wilson, D., Alm, J., Riutta, T., Laine, J., Byrne, K.A., Farrell, E.P., & Tuittila, E.-S. 2007. A high resolution green area index for modelling the seasonal dynamics of CO2 exchange in peatland vascular plant communities. *Plant Ecology* 190: 37–51.

Wilson, D., Blain, D., Couwenberg, J., Evans, C.D., Murdiyarso, D., Page, S.E., Renou-Wilson, F., Rieley, J.O., Sirin, A., Strack, M., & others. 2016. Greenhouse gas emission factors associated with rewetting of organic soils. *Mires and Peat* 17: 1–28.

Yu, Z.C. 2012. Northern peatland carbon stocks and dynamics: a review. *Biogeosciences* 9: 4071–4085.

Appendices

Appendix 1. Coefficients and R^2 values of correlations between LAI (m^2/m^2) and biomass (g/m^2).

Appendix 2. Average (± S.E.) length growth and biomass production of *Sphagnum* species during growing season 19.5.-7.9.2014.

Appendix 3. Parameter estimates of the linear mixed-effects model describing the differences in live standing biomass and biomass production between vegetation community types.

Appendix 4. Average (± standard error) live standing biomass of plant species and plant groups in different plant community types.

Appendix 5. Average (± standard error) biomass production of plant species and plant groups in different vegetation community types.

This article is protected by copyright. All rights reserved.

Accepted Article

Appendix 6. The relation of live standing biomass and biomass production to water table at the 18 sample plots.

Appendix 7. Average (± standard error) of live standing root biomass and root biomass production in differents depths below the moss capitula.

Appendix 8. Average vascular belowground to aboveground biomass ratio (AG:BG) in different vegetation community types for live standing biomass and biomass production.

Accepted Article

This article is protected by copyright. All rights reserved.

Accepted Article

Tables and figures

Table 1. Plant community types listed from driest to wettest with their mean water table (WT) (9.4.-24.9.2014), areal cover at the study site, the gravimetric content of P, N and C and the C:N ratio of surface peat (0-20 cm).

Community type	Vegetation composition	Mean WT (cm)	Areal cover (%)	P (%)	N (%)	C (%)	C:N
High hummock (HHU)	High cover of *Sphagnum fuscum* and dwarf-shrubs (*Empetrum nigrum, Calluna vulgaris, Betula nana*).	-25	14.0	0.019	0.87	47.56	57
Hummock (HU)	*Sphagnum fuscum* coverage of >10 %, *Eriophorum vaginatum* present, no dwarf-shrubs except *Andromeda polifolia*.	-13	7.4	0.008	1.51	71.91	76
High lawn (HL)	*Sphagnum rubellum* is the dominant moss species, *S. fuscum* coverage of <10 %.	-12	16.5	0.030	1.40	61.50	61
Lawn (L)	Moss layer dominated by *Sphagnum papillosum*, *S. magellanicum* and *S. balticum*.	-4	21.5	0.017	0.80	43.66	53
Hollow (HO)	Moss layer dominated by *Sphagnum majus* and *S. cuspidatum*. Field layer dominated by *Rhynchospora alba* and *Scheuchzeria palustris*.	-3	13.6	0.023	1.39	63.34	62
Bare peat (BP)	Ground layer consists mainly of bare peat without *Sphagna*. *Rhynchospora alba* is the dominant in field layer.	-1	15.3	0.026	1.68	47.95	29
Water (W)	Open water. The proportion of *Sphagna* or bare peat of the	-	11.6	-	-	-	-

This article is protected by copyright. All rights reserved.

ground layer is <10 %.						
Weighted average for the site (weighted by the cover of the community types)	-8		0.019	1.08	47.46	47.93

This article is protected by copyright. All rights reserved.

Table 2. Ecosystem level standing BM and BMP based on the areal cover of the plant community types at the study site. Other vascular plant species than sedges and dwarf-shrubs are included in the total vascular BM estimates. Error estimates are calculated as an average of community type standard errors weighted by the cover of each community type within the site.

	Standing BM		BM production	
	(g m^{-2})	% of total aboveground	(g m^{-2} growing season^{-1})	% of total aboveground
Total aboveground	140.9 ± 9.9		84.6 ± 8.0	
Sphagnum mosses	82.1 ± 3.5	58	41.1 ± 5.8	49
Vascular total	58.8 ± 9.8	42	43.5 ± 7.1	51
Dwarf-shrubs	32.9 ± 6.8	23	17.3 ± 3.7	20
Sedges	20.7 ± 5.2	15	20.7 ± 4.8	24
Other vasculars	5.2 ± 3.0	4	5.5 ± 3.0	7
		% of total belowground		% of total belowground
Total belowground	445.7 ± 118.3		47.0 ± 7.6	
Dwarf-shrubs	337.2 ± 111.2	76	25.4 ± 4.4	54
Sedges	108.6 ± 40.9	24	21.6 ± 6.2	46
		% of total		% of total
Total	586.6 ± 119.3		131.6 ± 14.5	
Sphagnum mosses	82.1 ± 3.5	14	41.1 ± 5.8	31
Vascular total	504.5 ± 119.9	86	90.5 ± 13.9	69
Dwarf-shrubs	370.1 ± 110.3	63	42.7 ± 7.5	32
Sedges	129.3 ± 41.5	22	42.3 ± 9.5	32
Other vasculars	5.1 ± 3.0	1	5.5 ± 3.0	4

This article is protected by copyright. All rights reserved.

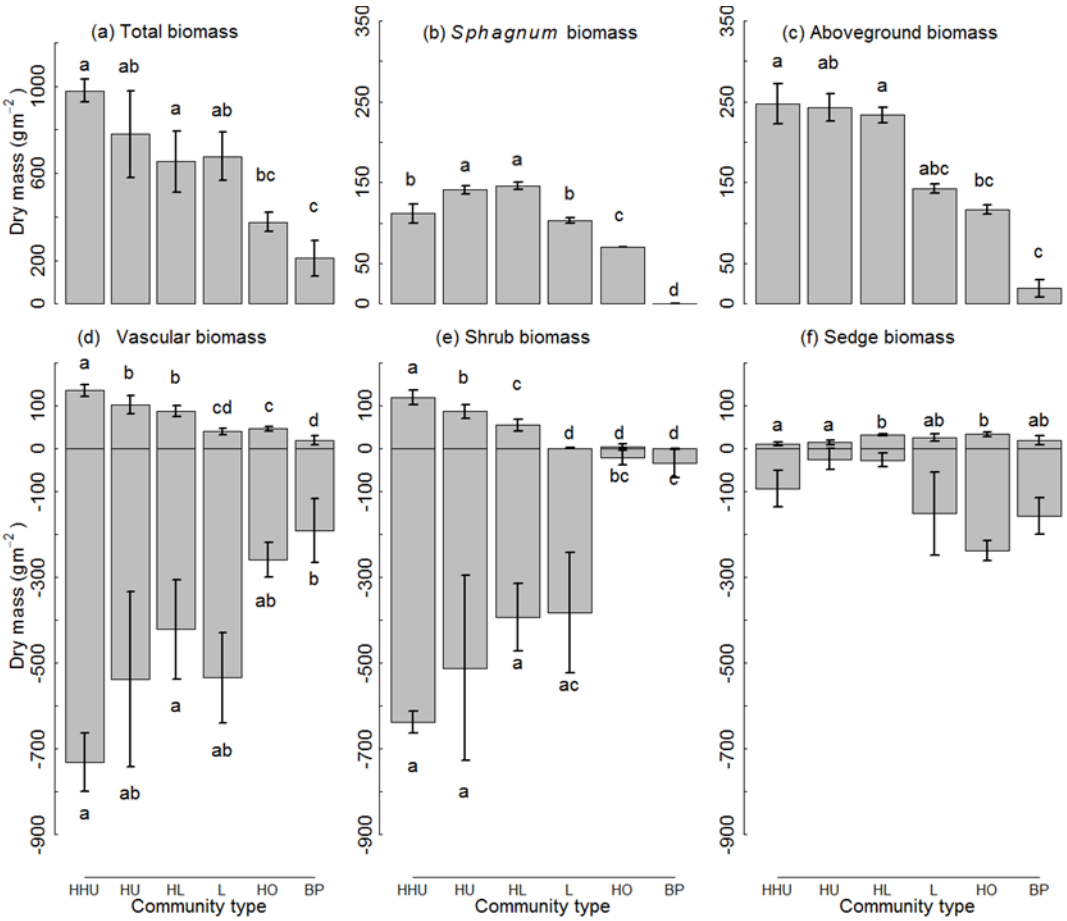


Figure 1. Average live standing biomass (BM) in different plant communities. BM of a) summed above- and belowground compartments, b) *Sphagna*, c) total aboveground vegetation, d) vascular plants above- and belowground, e) dwarf-shrubs above- and belowground and f) sedges above- and belowground. Negative values (1d-1e) represent belowground biomass and bars represent standard error. Lettering (a to d) indicates significantly different subsets ($p<0.05$) where letters in common represent homogeneous groups based on linear mixed effects models. One very high belowground biomass value is removed from the graph for visual reasons, but it is included in all of the analysis.

Accepted Article

This article is protected by copyright. All rights reserved.

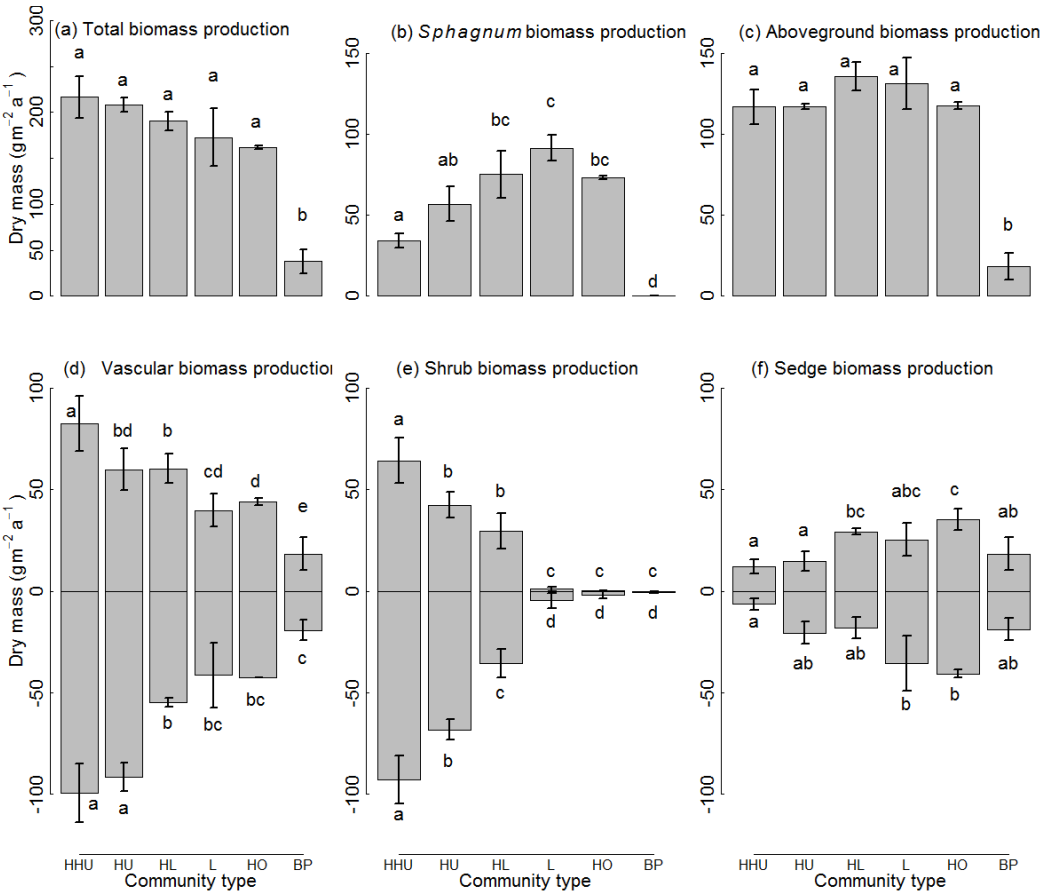


Figure 2. Average biomass production (BMP) in different vegetation communities. BMP of a) summed above- and belowground compartments, b) *Sphagna*, c) total aboveground vegetation, d) vascular plants above- and belowground, e) dwarf-shrubs above- and belowground and f) sedges above- and belowground. Bars represent standard error. Lettering (a to d) indicates significantly different subsets ($p<0.05$) where letters in common represent homogeneous groups according to the linear mixed-effects models.

This article is protected by copyright. All rights reserved.

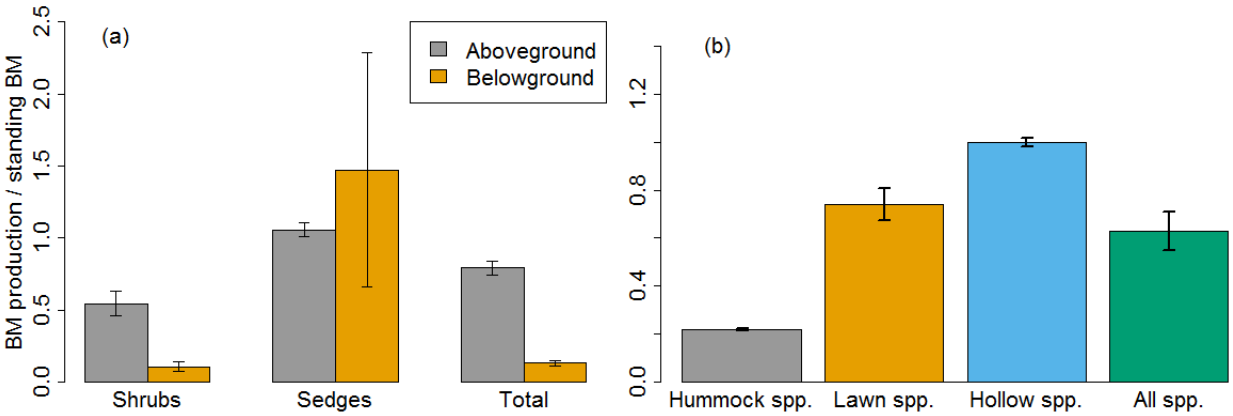


Figure 3. Average ratio (BMP:BM) of biomass production (BMP) to live standing biomass (BM) of (a) vascular plants above- and belowground and (b) *Sphagnum* species growing in different plant communities. Error bars represent standard error. Please note that the ratio in (b) describes *Sphagnum* production in relation to standing capitulum biomass.

Accepted Article

This article is protected by copyright. All rights reserved.