Moss production in a boreal, forestry-drained peatland

Raija Laiho[1], Paavo Ojanen[1], Mati Ilomets[2], Tomáš Hájek[3] and
Eeva-Stiina Tuittila[1]

[1] *Peatland Ecology Group, Department of Forest Sciences, P.O. Box 27, FI-00014 University of Helsinki, Finland (corresponding author, e-mail raija.laiho@helsinki.fi)*
[2] *Institute of Ecology, Tallinn University, Uus-Sadama 5, EE-10120 Tallinn, Estonia*
[3] *Institute of Botany of ASCR, Dukelská 135, CZ-379 82 Třeboň, Czech Republic*

Laiho, R., Ojanen, P., Ilomets, M., Hájek, T. & Tuittila, E.-S. 2011: Moss production in a boreal, forestry-drained peatland. *Boreal Env. Res.* 16: 441–449.

We studied the biomass production of moss species typical of pine-dominated drained peatland forests to evaluate their potential role in the carbon cycle of such sites. The study was carried out at two sites in Lakkasuo, central Finland. Prior to drainage, the sites had been mesotrophic and ombrotrophic. Shoots of *Pleurozium schreberi*, *Sphagnum angustifolium*, *S. fuscum*, *S. magellanicum* and *S. russowii* were marked in the autumn of 2004 and 2005, incorporated back in the original patches, recovered one year later, and measured for height growth, biomass, and biomass production. Biomass production varied from 16 to 388 g dry mass m^{-2} yr^{-1}. Both height growth and biomass production were higher at the mesotrophic site, while biomass estimates did not show distinct difference between sites. Variation in production within each dominant species was considerable. A simulation with our production values and published estimates of decomposition rates showed that these species have the potential to contribute significantly to soil carbon storage in drained peatlands.

Introduction

Sphagnum mosses play a major role in the carbon and element cycles in many boreal peatland ecosystems, especially those with an oligotrophic nutrient regime (Laiho *et al.* 2003, Malmer *et al.* 2003). Clymo (1998) estimated that globally, the total biomass of live *Sphagna* is 2.6 Pg dry mass. Production rates of the multitude of different *Sphagnum* species vary widely; however, methodological issues cause problems in the comparison of different studies (Lindholm and Vasander 1990). Decomposition rates also vary, but are generally low as compared with those of other plant groups even in the oxic surface peat layers (Dorrepaal *et al.* 2005, Bragazza *et al.* 2007),

and decrease further when the moss litter gets buried in the anoxic layers as a consequence of the height growth of the mosses. The persistence of *Sphagnum* necromass is one essential reason as to why peatland ecosystems act as sinks of atmospheric carbon.

About 10 million ha of peatland has been drained for forestry in northern Europe. In Finland alone, such areas total 4.8 million ha (Finnish Forest Research Institute 2009), which is half of the total peatland area in the country and constitutes about a quarter of its total forestry land. Forestry-drained peatlands are also found in the UK and North America. An early theory regarding the drainage succession of boreal peatlands suggested that mire species are gradually

replaced by forest species and *Sphagnum* mosses disappear from the vegetation (e.g. Tanttu 1915, Melin 1917, Sarasto 1961). During vegetation change, the composition of litter inputs changes from resistant *Sphagnum* litter to more easily decomposable forest litter. An increase in the aerobic layer thickness following water level draw-down leads to an increase in decomposition rates. These biotic and abiotic changes in the ecosystem, resulting in easily decomposable material together with more favorable conditions for decomposition, turn the ecosystem from a sink to a source of atmospheric carbon.

More recent results from drained peatlands, however, are in contrast with this theory. The work by Minkkinen and Laine (1998) suggested that sites characterized by stands of Scots pine (*Pinus sylvestris*) may remain carbon sinks even after long-term (5 decades) drainage. So far, it has been assumed that increased tree litter inputs would explain the continued carbon sink function (Minkkinen and Laine 1998, Domisch *et al.* 2000). Even though it has been observed that great changes may take place in the moss community composition, *Sphagnum* mosses may remain as a major group in drained pine-dominated peatlands (Laine *et al.* 1995). This has been largely overlooked, even though a first evaluation of plant-mediated carbon cycling in drained peatlands that involved all vegetation layers suggested that the moss layer may retain its major role (Laiho *et al.* 2003).

Contemporary knowledge on directional drainage succession in peatlands suggests that moss species adapted to wet conditions (lawns, hollows) give way to species typical of dry conditions (hummocks): forest mosses such as *Pleurozium schreberi*, or hummock *Sphagnum* species, such as *S. magellanicum*, *S. russowii* and *S. fuscum*. Hummock species have previously been found to decompose at slower rates than hollow species, despite the relatively dry, oxic conditions in hummocks (Belyea 1996, Turetsky *et al.* 2008). Such mosses could thus play a role in the carbon sink function of drained peatlands, but this role would depend on the range of their production potential. Variation in the moss layer might explain some of the variation in the sink/source function that has been reported for

peatland forests (Minkkinen and Laine 1998). With a few exceptions, there is little information on moss production in drained peatlands (*see* Vasander 1982, Reinikainen *et al.* 1984).

The aim of this study was to evaluate the production of moss species typical of drained peatland forests. We chose our study sites to represent peatlands with favourable conditions for moss growth: pine-dominated sites with such nutrient regimes that drainage would not induce replacement of mosses by lichens (as is the case in extremely poor bogs: Vasander 1982, Jauhiainen *et al.* 2002). We discuss the potential role of the mosses in the carbon cycle of the drained peatland forests.

Material and methods

Study site

Our study site was the Lakkasuo peatland located in Orivesi, central Finland (61°48´N, 24°19´E, ca. 150 m a.s.l.). It is a raised bog complex with a large minerotrophic lagg (Laine *et al.* 2004). About half of this peatland was drained for forestry in 1961. We chose two sites located in the drained part: one that had been a mesotrophic sedge fen before the drainage, and one that had been an ombrotrophic bog with a hummock-hollow microrelief. These sites are hereafter referred to as "mesotrophic" and "ombrotrophic". At the time of our measurements (2004–2006), both sites supported a tree stand dominated by Scots pine, about 2.5 kg m^{-2} total tree biomass in the ombrotrophic site and 8 kg m^{-2} in the mesotrophic site (Anttila 2008). There was a mixture of pubescent birch (*Betula pubescens*) at the mesotrophic site. Other vascular vegetation at the mesotrophic site consisted mainly of shrubs, such as *Vaccinium myrtillus*, *V. vitis-idaea* and *Empetrum nigrum*, plus some herbs, such as *Trientalis europaea* and small *Dryopteris carthusiana*, and at the ombrotrophic site, shrubs, such as *Ledum palustre*, *V. uliginosum* and *E. nigrum*, plus some cottongrass *Eriophorum vaginatum*. The bottom layer was dominated by different *Sphagnum* moss species and by feathermoss *Pleurozium schreberi* (Table 1). In addition to

the dominant species, *Dicranum polysetum* and *Polytrichum strictum* were also found.

We marked 23 measurement points (hereafter called "locations") at the mesotrophic site, and 33 measurement points at the ombrotrophic site. We chose areas with healthy patches dominated by different moss species typical of the sites (Table 1). The higher number of locations in the ombrotrophic site was due to its higher number of species. Each location was marked with a perforated plastic pipe for measuring the water table level (WT). The relative WT at each location was estimated by calculating the mean of two WT measurements (4 October 2005 and 13 August 2006; the purpose was to relate the distance of the locations from the WT to each other, not to describe the wetness of the locations for which this *n* is too small).

Air temperature and relative humidity at 2-m height, and photosynthetically active radiation (PAR) were measured at 1-h intervals by an automatic weather station located at an open treeless site at the undrained part of the peatland. Precipitation was measured during the May–October period when precipitation occurs as rainfall. Water levels were monitored over the frost-free season in the vicinity of both our sites using Ott plotters (Kempten, Germany).

Moss production

We applied the marking method developed by Ilomets (1974). At each location, a handful of mosses was carefully extracted, and a minimum of 20 individual shoots were selected for marking while the rest were put aside. On each shoot, a mark was made on the stem, 20 mm below the apical point, with a non-toxic, fast drying nitrocellulose paint. Then, the handful of now both marked and unmarked shoots was carefully reconstructed and returned to the spot from where it was extracted. Marking was done in autumn (late September 2004, early October 2005) to ensure that the moisture conditions were favourable for the recovery of the manipulated shoots. We deemed that we were successful in this since at the time of harvest, it was impossible to distinguish the manipulated spots from the surrounding undisturbed moss patches without a detailed description of their location.

The marked shoots were harvested after one year. The shoot was cut at a point 20 mm below the apical point, and also at the mark made the year before. The length of this segment represented the height growth of the shoot. Biomass production consisted of these stem segments plus any secondary shoots that had developed above the initial 20-mm mark. These were pooled per species and location, weighed after drying at 105 °C, and biomass production by shoot was calculated by dividing the total mass with the number of measured shoots. The 20-mm stem tops including the primary capitula were also pooled per species and location, dried and weighed. The dry mass of the 20-mm stem tops was added to the production samples to provide an estimate of total biomass. Average height growth was calculated for each species at each location.

In May 2006, a 21-cm^2 sample from the same moss patch where the marking was done was collected from each location. These samples were separated by species, and the number of shoots per species was counted to provide an estimate of the number of shoots per unit area. For each species and location, total biomass production

Table 1. Number of measurement points (locations) for each dominant species in 2005 and 2006 at the mesotrophic and ombrotrophic sites. WT = relative water table depth (cm) for the 2006 locations. 2005 & 2006 = number of locations for which measurements were obtained in both years. *S.* = *Sphagnum*, *P.* = *Pleurozium*.

Dominant species	2005	2006	2005 & 2006	WT
S. magellanicum	4	4	4	–53
S. angustifolium	4	7	4	–37
S. russowii	4	6	4	–48
P. schreberi	0	5	0	–43
All mesotrophic	12	22	12	–50
S. magellanicum	4	5	3	–39
S. angustifolium	6	8	6	–26
S. russowii	1	3	1	–45
S. fuscum	9	9	8	–32
P. schreberi	4	7	4	–31
All ombrotrophic	24	32	22	–42
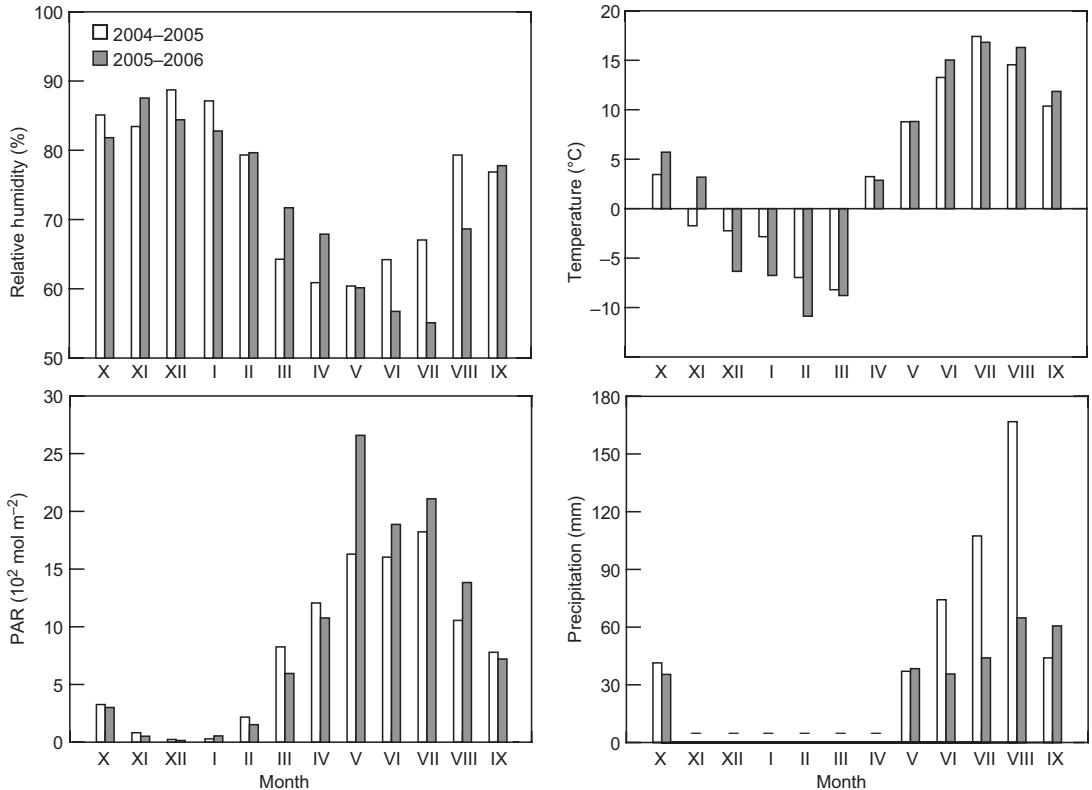
Fig. 1. Weather statistics at the Lakkasuo automatic weather station for November–October periods of the years 2004–2005 and 2005–2006. Values of air temperature and relative humidity are monthly means and values of photosynthetically active radiation (PAR) and precipitation are monthly sums.

(g dry mass m^{-2} yr^{-1}) and total biomass (g dry mass m^{-2}) per unit area were calculated by multiplying the production and total biomass per shoot by the number of shoots. Production and biomass of all the species were then summed up for each location. Biomass turnover was calculated for each location as production/total biomass (yr^{-1}).

Numerical analyses

We tested with a general linear model whether variation in production could be explained by the dominant species, site (trophic level), year or WT. For that purpose, a model with production (g dry mass m^{-2} yr^{-1}) as the dependent variable, year, site and dominant species as fixed factors, WT as a fixed covariate, and measurement location as a random factor was constructed using Systat 12 (Systat Software, Inc.).

Results

There was a marked difference between the growing seasons (May–October) of 2005 and 2006 (Fig. 1). During the growing season of 2006, Lakkasuo received 26% more PAR and 41% less rain than during the growing season of 2005. Air temperature was somewhat higher (12.4 °C *vs.* 11.3 °C) and relative humidity somewhat lower (67% *vs.* 72%). The differences were reflected in summertime water levels at both sites (Fig. 2).

Moss biomass production varied from 16 to 388 g m^{-2} yr^{-1} (Table 2). It had a mean of 109 g m^{-2} yr^{-1} in 2005 and 161 g m^{-2} yr^{-1} in 2006. In both years, production was higher at the mesotrophic site (Table 2 and Fig. 3); only the *Pleurozium schreberi* dominated locations in 2006 showed virtually equal production at the mesotrophic and the ombrotrophic sites. Moss
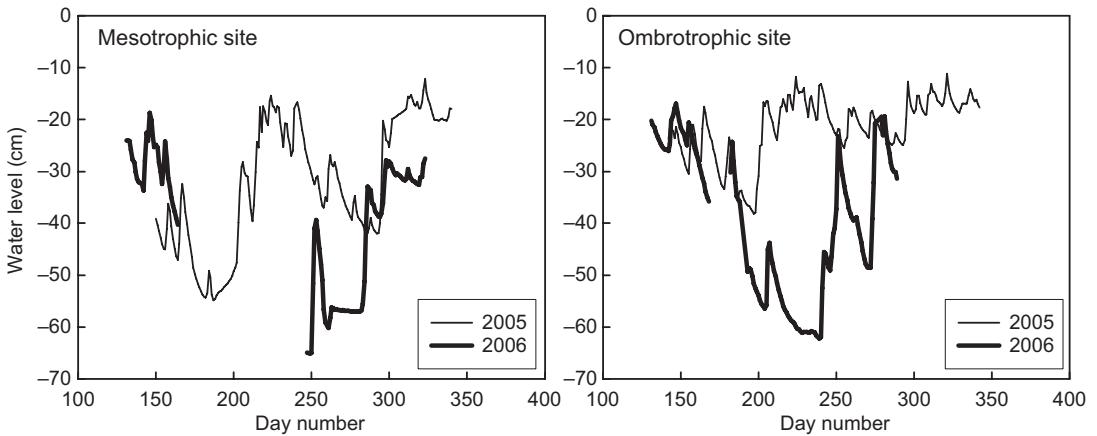
Fig. 2. Water levels relative to soil surface (cm) of the sites in 2005 and 2006. Day 150 = 30 May, day 300 = 27 October.

biomass had a mean of 362 g m^{-2} in 2005 and 363 g m^{-2} in 2006 and did not show distinct difference between sites. Thus, turnover was higher at the mesotrophic site and in 2006, having an overall mean of 0.32 yr^{-1} in 2005 and 0.45 yr^{-1} in 2006 (Table 2).

The rates of production differed between years ($p < 0.0001$) and sites ($p = 0.0045$) (Table 3). WT was not significant in explaining variation in production. In general, production did not depend on the dominant species; only the *Sphagnum angustifolium* dominated loca-

Table 2. Mean, minimum and maximum of production (g dry mass m^{-2} yr^{-1}), biomass (g dry mass m^{-2}) and turnover (yr^{-1}) of locations with different dominant species in 2005 and in 2006. *S.* = *Sphagnum*, *P.* = *Pleurozium*.

Dominant species	Production			Biomass			Turnover		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
2005 all locations	109	19	252	362	123	775	0.32	0.04	0.69
Mesotrophic all	155	59	252	388	225	612	0.40	0.21	0.55
S. magellanicum	123	59	252	406	280	612	0.28	0.21	0.41
S. angustifolium	168	121	236	395	255	535	0.44	0.31	0.51
S. russowii	174	96	208	365	225	452	0.47	0.43	0.55
Ombtrotrophic all	86	19	149	349	123	775	0.28	0.04	0.69
S. magellanicum	51	19	72	175	123	253	0.31	0.12	0.45
S. angustifolium	113	64	149	371	202	436	0.31	0.15	0.41
S. russowii	40	40	40	198	198	198	0.20	0.20	0.20
S. fuscum	87	22	133	406	192	619	0.26	0.04	0.69
P. schreberi	92	42	146	402	260	775	0.26	0.15	0.50
2006 all locations	161	16	388	363	79	620	0.45	0.13	0.69
Mesotrophic all	202	43	388	368	79	620	0.55	0.35	0.69
S. magellanicum	276	145	388	476	343	576	0.56	0.42	0.67
S. angustifolium	211	115	346	401	244	620	0.52	0.42	0.62
S. russowii	204	82	327	356	226	525	0.56	0.35	0.68
P. schreberi	128	43	187	253	79	542	0.56	0.35	0.69
Ombtrotrophic all	133	16	264	360	116	580	0.38	0.13	0.62
S. magellanicum	109	16	163	294	114	536	0.36	0.14	0.50
S. angustifolium	161	55	221	366	254	505	0.45	0.16	0.62
S. russowii	92	65	124	281	173	337	0.34	0.27	0.37
S. fuscum	140	73	264	440	278	580	0.34	0.13	0.57
P. schreberi	126	55	189	332	223	439	0.39	0.13	0.53
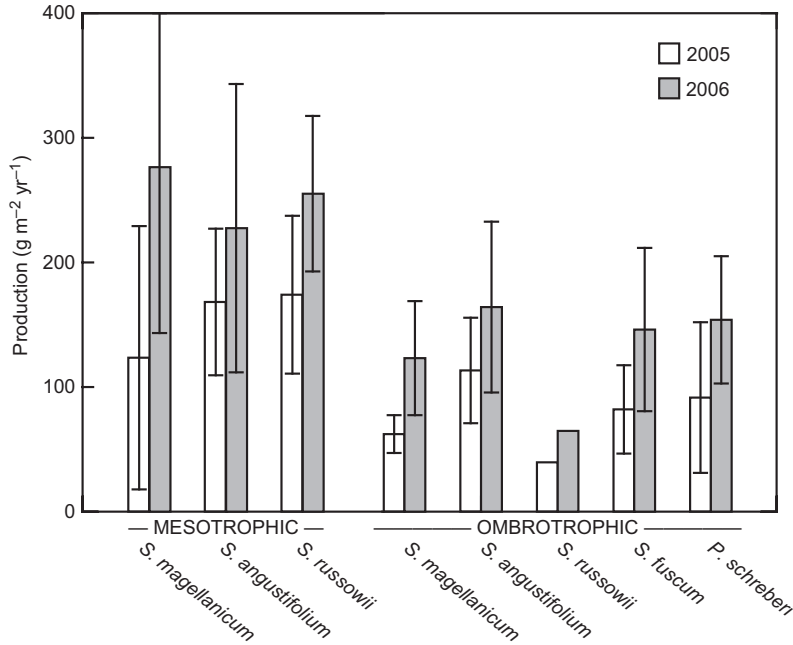
Fig. 3. Mean moss biomass production ± SD (g dry mass m⁻² yr⁻¹) according to dominant moss species in 2005 and 2006 for locations that were harvested in both years. All moss species growing in the same location are included. *S. = Sphagnum*, *P. = Pleurozium.*

tions differed from the less productive *Pleurozium schreberi* dominated locations. Variation in production between locations of each dominant species was considerable at both sites (Table 3 and Fig. 3), and thus r^2 of the model was no more than 0.343.

Similarly to production, moss height growth was also higher at the mesotrophic site and in 2006 (Fig. 4). In 2005, height growth had a mean value of 22 mm yr⁻¹ at the mesotrophic site and 13 mm yr⁻¹ at the ombrotrophic site. In 2006,

the respective means were 36 mm yr⁻¹ and 20 mm yr⁻¹. A patch of *S. magellanicum* growing on a mesotrophic location had the overall highest height growth: 74 mm yr⁻¹ in 2006.

Production per unit height growth was quite similar at the mesotrophic and ombrotrophic sites and in 2005 and 2006. Mean production per height growth was 7.1 g m⁻² mm⁻¹ at the mesotrophic site and 6.5 g m⁻² mm⁻¹ at the ombrotrophic site in 2005, and 5.7 g m⁻² mm⁻¹ and 6.8 g m⁻² mm⁻¹ in 2006, respectively.

Table 3. The effect and significance of different potential explainers of moss production, as found with a mixed linear model with biomass production (g dry mass m⁻² yr⁻¹) as the dependent variable, year, site and dominant species as fixed factors, relative water table (WT, cm) as a fixed covariate and measurement location (p = 0.0218) as a random factor.

Effect	Level	Estimate	SE	d.f.	t	p
Intercept		88.3	54.8	49	1.61	0.114
Year	2005	−59.9	11.2	33	−5.34	< 0.001
	2006	Effect included in the intercept				
WT		−0.426	1.261	33	−0.338	0.738
Site	mesotrophic	61.6	20.2	33	3.053	0.004
	ombrotrophic	Effect included in the intercept				
Dominant species	*S. magellanicum*	24.6	26.1	33	0.944	0.352
	S. angustifolium	53.1	23.2	33	2.285	0.029
	S. russowii	20.1	27.5	33	0.728	0.472
	S. fuscum	36.9	26.1	33	1.415	0.166
	P. schreberi	Effect included in the intercept				
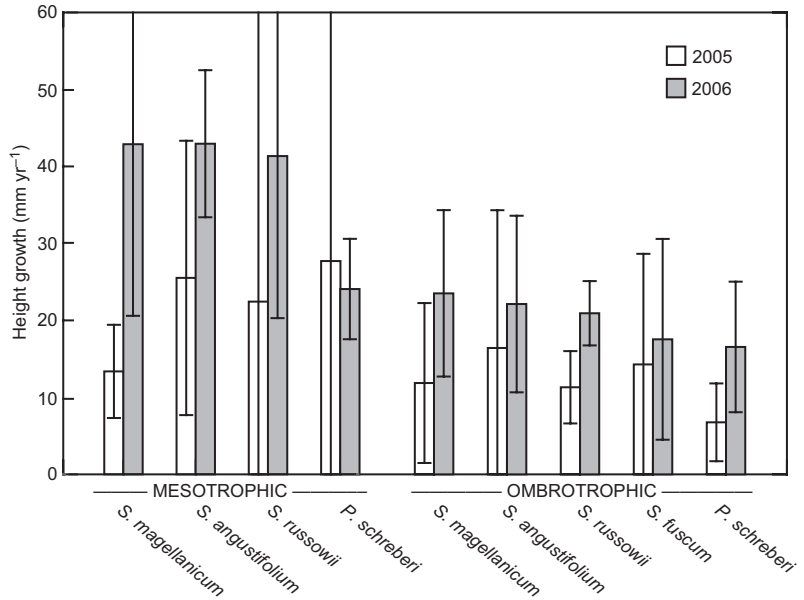
Fig. 4. Mean height growth ± SD (mm yr⁻¹) of different moss species in 2005 and 2006 at the mesotrophic and the ombrotrophic sites. *S.* = *Sphagnum*, *P.* = *Pleurozium*.

Discussion

The range of production values that we observed was 16–388 g dry mass m^{-2} yr^{-1}, and both the minimum and the maximum were recorded for the same species, *S. magellanicum*. In 2005, the production values were slightly lower than those found at undrained sites in the same region in a study that covered a time period of over 3 years (Lindholm and Vasander 1990). However, in 2006, the values were closely comparable to *Sphagnum* production in undrained conditions. It must be borne in mind in all comparisons that our estimates are not spatially representative but reflect only production in fully moss-covered patches. In practice, there were no moss-free surfaces in the ombrotrophic site, whereas in the mesotrophic one, such surfaces occurred where birch leaf litter was abundant.

Water table depth shows a high between-site variation in boreal peatlands drained for forestry (Ojanen *et al*. 2010). Our study sites can be considered typical examples of successful ditching: water table depth varied depending on rainfall but generally remained at or deeper than 20 cm below the soil surface, even during most of the rainy growing season of 2005.

The pre-drainage trophic level had the clearest overall influence on moss production: pro-

duction was 78% and 52% higher at the mesotrophic site in 2005 and 2006, respectively. Even though the ground water and nutrient inputs to the initially mesotrophic site have likely decreased because of the ditches, there was still a difference in the soil nutrient status of the sites. Soil analyses carried out in the vicinity of our sites (*see* Jaatinen *et al*. 2007) indicated that contents of N, P and base cations were about 1.5 times higher in the surface peat (0–10 cm) of our mesotrophic site as compared with those in the ombrotrophic one.

Interspecies differences were not statistically significant in our study; however, the number of observations per species was rather low when considering the high variation within each species.

It was somewhat surprising that the distance to water table level did not influence moss production. We expected production to be higher in locations with the water table closer to the surface. In fact, the ombrotrophic site, with somewhat higher average water levels, showed lower moss production. Within sites, there was no correlation between WT and moss production. On the other hand, variation in WT within sites was moderate, which is typical after drainage. During drainage succession, micro-topographical variation is reduced, which is also shown

in changes in vegetation composition (disappearance of hollow species and proliferation of hummock species; Laine *et al*. 1995). According to Verry (1997), peat soils generally have a capillary fringe that reaches the surface when the water table is within 30–40 cm; in highly decomposed soils it may reach the surface when the water table is within 60 cm. In summer 2006, water levels in both sites were probably too deep for the capillary fringe to reach the surface. However, outside the summer months they were within the suggested limits. Generally, *Sphagnum* mosses grow more during spring and autumn periods with cool and moist conditions than in summers with warm and dry conditions (Gunnarsson 2005).

The higher production in the drier year of the study could indicate that a lack of soil moisture may not generally restrict *Sphagnum* growth in drained peatlands. Instead, the moss layer was able to utilize the higher availability of photosynthetically active radiation (PAR). A mean ratio of precipitation to temperature of 6.5 mm/°C during May–September triggered an irreversible desiccation of *Sphagnum* mosses in the Italian Alps (Bragazza 2008). Conditions in our sites were at the limit, namely 6.3 mm/°C, in 2005, and clearly below that (3.7 mm/°C) in 2006; yet, mosses were still able to reach substantial rates of production. This may mean that moss species typical of open pristine peatlands *versus* more shaded drained peatlands may respond differently to variations in environmental conditions (*see* also Hájek *et al*. 2009). It should be noted that all *Sphagnum* species found in our sites occur on hummock surfaces under pristine conditions. Hummock species have a large tolerance to WT in comparison with species characteristic of wetter conditions that are more specialised (Väliranta *et al*. 2007), mainly due to large morphological plasticity enhancing water retention in desiccated microhabitats.

Differences in production between sites and years corresponded to differences in height growth. The mosses in this study seemed to react to varying growing conditions with varying height growth, which then resulted in varying biomass production. Mosses at the ombrotrophic site actually had more biomass in capitula than those of the mesotrophic site, which resulted in smaller differences between sites in biomass than in biomass production. Since all our biomass estimates consisted of the production of the previous year, in addition to the 20-mm shoot tips, they may not correspond to actual (functional) biomass of all species. However, the limit between live and dead shoot parts is generally not clear, and thus, biomass and turnover estimates may vary between studies.

Our method, which involved the extraction of the sample moss shoots may appear radical. However, it has the advantage that only a minor part of the moss patch is disturbed and thus, it is easy to determine whether the treated shoots differ from the undisturbed neighbours. We concluded that the method worked well and has given realistic results, since it was impossible to observe any difference in the disturbed shoots as compared to the surrounding patch at the time of recovery. We carried out the marking in the autumn when the moss layer was moist; during a dry spell, the chance of the extracted shoots losing capillary contact and segregating from the surrounding patch would probably be much higher.

Decomposition data for mosses in drained peatlands are scarce. We calculated decomposition rates for *S. magellanicum* (k = 0.078), *S. russowii* (0.064) and *P. schreberi* (0.233) using mass loss data for these species in drained conditions presented by Laiho *et al*. (2008). To estimate organic matter accumulation potential of these species, we carried out a 40-year simulation using these decomposition rates, and the 2006 production values from the mesotrophic site as annual litter production for each simulated year. At the end of the simulation, almost 0.5 kg m^{-2} remained of *P. schreberi* (values converging at about 25 years), and about 3 kg m^{-2} of both *S. magellanicum* and *S. russowii* (values still increasing at the end of simulation). Such a simulation is not very realistic, of course, but in any case it shows that the potential of these species to contribute quite significantly to soil C storage in drained peatlands should not be ignored.

References

Belyea L.R. 1996. Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. *Oikos* 77: 529–539.

Bragazza L. 2008. A climatic threshold triggers the die-off of peat mosses during an extreme heat wave. *Global Change Biol.* 14: 2688–2695.

Bragazza L., Siffi C., Iacumin P. & Gerdol R. 2007. Mass loss and nutrient release during litter decay in peatland: The role of microbial adaptability to litter chemistry. *Soil Biol. Biochem.* 39: 257–267.

Clymo R.S. 1998. *Sphagnum*, the peatland carbon economy, and climate change. In: Bates J.W., Ashton N.W. & Duckett J.G. (eds.), *Bryology for the twenty-first century*, British Bryological Society, pp. 361–368.

Domisch T., Finér L., Laiho R., Karsisto M. & Laine J. 2000. Decomposition of Scots pine litter and the fate of released carbon in pristine and drained pine mires. *Soil Biol. Biochem.* 32: 1571–1580.

Dorrepaal E., Cornelissen J.H.C., Aerts R., Wallén B. & van Logtestijn R.S.P. 2005. Are growth forms consistent predictors of leaf litter quality and decomposability across peatlands along a latitudinal gradient? *J. Ecol.* 93: 817–828.

Finnish Forest Research Institute 2009. *Finnish Statistical Yearbook of Forestry*. Finnish Forest Research Institute, Vantaa, Finland.

Gunnarsson U. 2005. Global patterns of Sphagnum productivity. *J. Bryol.* 27: 269–279.

Hájek T., Tuittila E.-S., Ilomets M. & Laiho R. 2009. Light responses of mire mosses — a key to survival after water-level drawdown? *Oikos* 118: 240–250.

Hobbie S.E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol. Monogr.* 66: 503–522.

Ilomets M. 1974. Some aspects of measuring the growth of *Sphagnum*. In: Kumari E. (ed.), *Estonian wetlands and their life*, Est. Contr., IBP 7, Valgus, Tallinn, pp. 191–203.

Jaatinen K., Fritze H., Laine J. & Laiho R. 2007. Effects of short- and long-term water-level drawdown on the populations and activity of aerobic decomposers in a boreal peatland. *Global Change Biol.* 13: 491–510.

Jauhiainen S., Laiho R. & Vasander H. 2002. Ecohydrological and vegetational changes in a restored bog and fen. *Ann. Bot. Fennici* 39: 185–199.

Johnson L.C. & Damman A.W.H. 1991. Species-controlled *Sphagnum* decay on a South Swedish raised bog. *Oikos* 61: 234–242.

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. *Global Biogeochem. Cycles* 17(2), 1053, doi:10.1029/2002GB002015.

Laiho R., Minkkinen K., Anttila J., Vávrová P. & Penttilä T. 2008. Dynamics of litterfall and decomposition in peatland forests: Towards reliable carbon balance estimation? In: Vymazal J. (ed.), *Wastewater treatment, plant dynamics and management in constructed and natural wetlands*, Springer Science + Business Media, Dordrecht, pp. 53–64.

Laine J., Vasander H. & Laiho R. 1995. Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *J. Appl. Ecol.* 32: 785–802.

Lindholm T. & Vasander H. 1990. Production of eight species of *Sphagnum* at Suurisuo mire, southern Finland. *Ann. Bot. Fennici* 27: 145–157.

Malmer N., Albinsson C., Svensson B.M. & Wallén B. 2003. Interferences between *Sphagnum* and vascular plants: effects on plant community structure and peat formation. *Oikos* 100: 469–482.

Melin E. 1917. Studier over de norrländska myrmarkernas vegetation med särskilt hänsyn till deras skogsvegetation efter torrläggning. *Norrländskt handbibliotek* 7: 1–426.

Minkkinen K. & Laine J. 1998. Long-term effect of forest drainage on the peat carbon stores of pine mires in Finland. *Can. J. For. Res.* 28: 1267–1275.

Ojanen P., Minkkinen K., Alm J. & Penttilä T. 2010. Soil–atmosphere CO_2, CH_4 and N_2O fluxes in boreal forestry-drained peatlands. *For. Ecol. Manage.* 260: 411–421.

Reinikainen A., Vasander H. & Lindholm T. 1984. Plant biomass and primary production of southern boreal mire-ecosystems in Finland. *Proceedings of the 7th International Peat Congress*, International Peat Society, the Irish National Peat Committee, Dublin, pp. 1–20.

Sarasto J. 1961. Über die Klassifizierung der für Walderziehung entwässerte Moore. *Acta Forestalia Fennica* 74(5): 1–57.

Tanttu A. 1915. Tutkimuksia ojitettujen soiden metsittymisestä. *Acta Forestalia Fennica* 5(2): 1–245.

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. *J. Ecol.* 96: 1297–1305.

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

Väliranta M., Korhola A., Seppä H., Tuittila E.-S., Sarmaja-Korjonen K., Laine J. & Alm J. 2007. High resolution reconstruction of wetness dynamics in a southern boreal raised bog during the late Holocene. *Holocene* 17: 1093–1107.