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# *SPHAGNUM* ECOPHYSIOLOGY OF RESTORED, DRAINED, AND PRISTINE BOREAL SPRUCE SWAMP FORESTS

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## SUMMARY

Boreal spruce swamp forests, in their natural state, harbor a large diversity of plant species. However, these swamp forests have been heavily exploited for forestry; in southern Finland for example, 60% to 80% of the original spruce swamp forests have been drained since the 1950s. In recent years, however, restoration of drained spruce swamps has been taking place. As *Sphagnum* mosses are keystone species in spruce swamp habitats, this study seeks to evaluate the effect of restoration on the ecophysiological functioning of *Sphagnum* mosses in comparison to pristine and drained sites. Ecophysiological parameters varied strongly between species, with species of wetter habitats exhibiting higher potential photosynthesis rates and lower stress levels, as indicated by chlorophyll fluorescence. Potential photosynthesis was also greatest in restored sites.

KEYWORDS: Photosynthesis, mire, peatland, moss

## INTRODUCTION

Spruce swamp forests in Finland have become threatened habitats largely as a result of extensive drainage for forestry (Raunio *et al*., 2008). Drainage changes the balance between the treed overstory and the peat-forming *Sphagnum* carpet found in pristine spruce mires. With drainage, tree production increases, but the drier conditions are unfavorable for *Sphagnum* growth (Laine *et al.*, 1995). The goal of restoration is to re-establish the tree-moss balance, as *Sphagnum* mosses are not only important in peat-development, but also in creating moist microclimates for other plant species, animals and fungi (Dioumaeva *et al.*, 2002). The objective of this study was to evaluate the effects of forestry-drained spruce mire restoration on the ecophysiological functioning of *Sphagnum* mosses.

## METHODS

We compared parameters of photosynthetic $CO_2$ exchange and chlorophyll fluorescence of the dominant *Sphagnum* mosses across 3 restored, 3 drained, and 3 pristine spruce mires in southern Finland monthly during the summer of 2011 (Fig.1). Three replicates of three to four of the dominant *Sphagnum* species were collected from their optimal microhabitats from each site, with *Pleurozium schreberi* and *Sphagnum girgensohnii* collected from all sites regardless of dominance. In May, a total of four to six species per site were measured to assess the diversity in species response.

A portable gas exchange fluorescence system GFS-3000 (Heinz Walz GmbH, Effeltrich, Germany) was used to measure net $CO_2$ assimilation rate ($A$) at four different levels of photosynthetic photon flux density (PPFD), decreasing in order from 1000, 50, 25, to 0 µmol $m^{-2}s^{-1}$ (abbreviated as $A_{1000}$, $A_{50}$, $A_{25}$, and $A_0$ as dark respiration and expressed per unit dry mass – mg $g^{-1}$ $h^{-1}$). During the measurement period, other environmental conditions within the cuvette were kept constant. Measurements of quantum yield of PSII were taken at the end of the 1000 µmol $m^{-2}s^{-1}$ light level. Samples were then dark-acclimated for at least 6 hours, after which variable ($F_v$) and maximum fluorescence ($F_m$) were measured, used to calculate the ratio $F_v/F_m$ as an indicator of stress response at PSII. We also calculated the maximum quantum yield of $CO_2$ assimilation ($\alpha$) as $(A_{25}- A_0)/$ 25 µmol $m^{-2}s^{-1}$. Light compensation point ($PPFD_c$) of $A$ was calculated as $x$-intercept of the initial part of $A$/PPFD curve.

Site water table was measured during each sampling period from 4 wells that transected the centre of the site. In addition, at each point of moss collection, peat moisture of the top 12cm was measured using a CS-620 HydroSense (Campbell Scientific, Utah, USA) moisture meter.

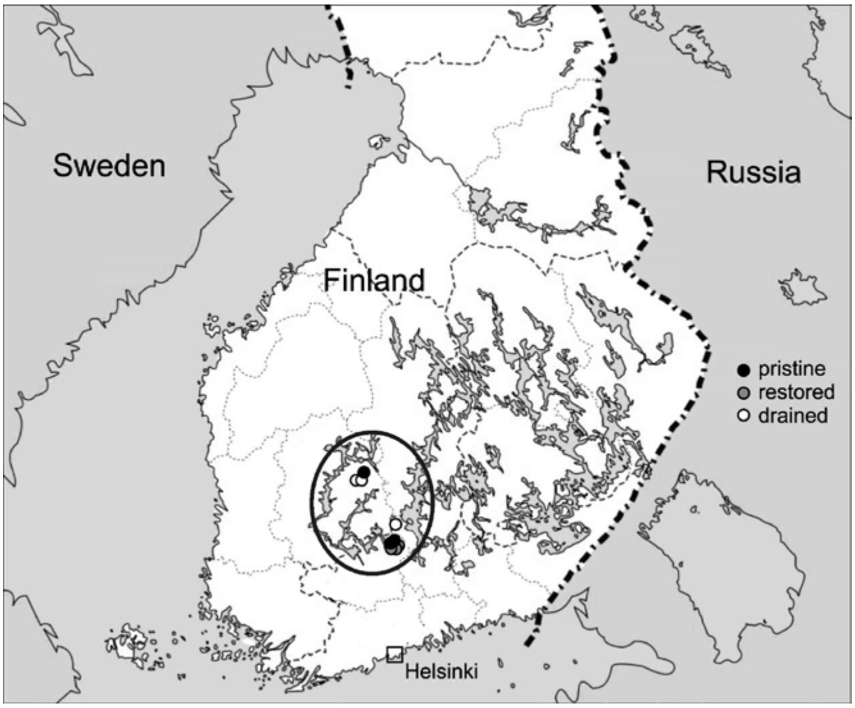


Fig. 1: Location of the study sites.

### Statistical analyses

Indirect ordination analysis (PCA) was used to assess patterns in ecophysiological parameters during the month of May in relation to treatment type, moss species, site water table, and peat moisture.

Direct gradient analysis using redundancy analysis (RDA) was used to hierarchical partition the variation of ecophysiological variables. We conducted a series of (partial) RDA where the variance components higher in the hierarchy were taken as co-variables. The hierarchical order of variance components is shown in Table 1. As additional species were measured in May, only the species measured in all months were included in the RDA analysis. CANOCO for Windows 4.52 was used for analysis (ter Braak and Šmilauer, 2002).

## RESULTS

Ecophysiological parameters varied strongly between species, treatment, and time of year, with measured environmental variables explaining 68.8% of the variation (Table 1). Ordination of parameters measured in May clearly illustrate a diversity in species response (Fig. 2). *Sphagnum* species formed a linear gradient according to potential photosynthesis rate ($A_{1000}$) and stress level, indicated by $\alpha$ and $F_v/F_m$. Species in wetter microhabitats, notably *Sphagnum riparium*, had the highest $A_{1000}$. Wet habitat species also exhibited less stress. Feather mosses, common to the driest microhabitats, differed from *Sphagnum* species by exhibiting higher respiration and lower light compensation points.

Table 1. Hierarchical partitioning of ecophysiological parameters based on a series of redundancy analyses. In each analysis the variables above were taken as co-variables.

| Source of variation | Amount of variation explained (%) | *F*-value | *P*-value |
|---|---|---|---|
| Season | 16.7 | 25.3 | 0.002 |
| Species | 37.0 | 59.9 | 0.002 |
| Treatment | 3.8 | 8.2 | 0.002 |
| Treatment × Species | 1.6 | 1.6 | 0.026 |
| Treatment × Season | 4.3 | 3.5 | 0.002 |
| Season × Species | 4.3 | 2.8 | 0.002 |
| Site water table | 0.6 | 5.1 | 0.002 |
| Peat field moisture | 0.5 | 4.2 | 0.008 |
| **Total** | **68.8** | | |

May differed from the later months ecophysiologically, exhibiting lower potential photosynthesis and and higher light compensation points. Differences between the remaining months, however, were not strong. Considering the effect of species across all months, the strongest gradient separated *Sphagnum* mosses from *Pleurozium schreberi* with lowest productivity. However, the amount of variation explained in the axis separating all *Sphagnum* species was not strong. When species and season were taken into account, treatment type had a small direct effect on moss ecophysiology, and explained only four percent of total variation (Table 1).

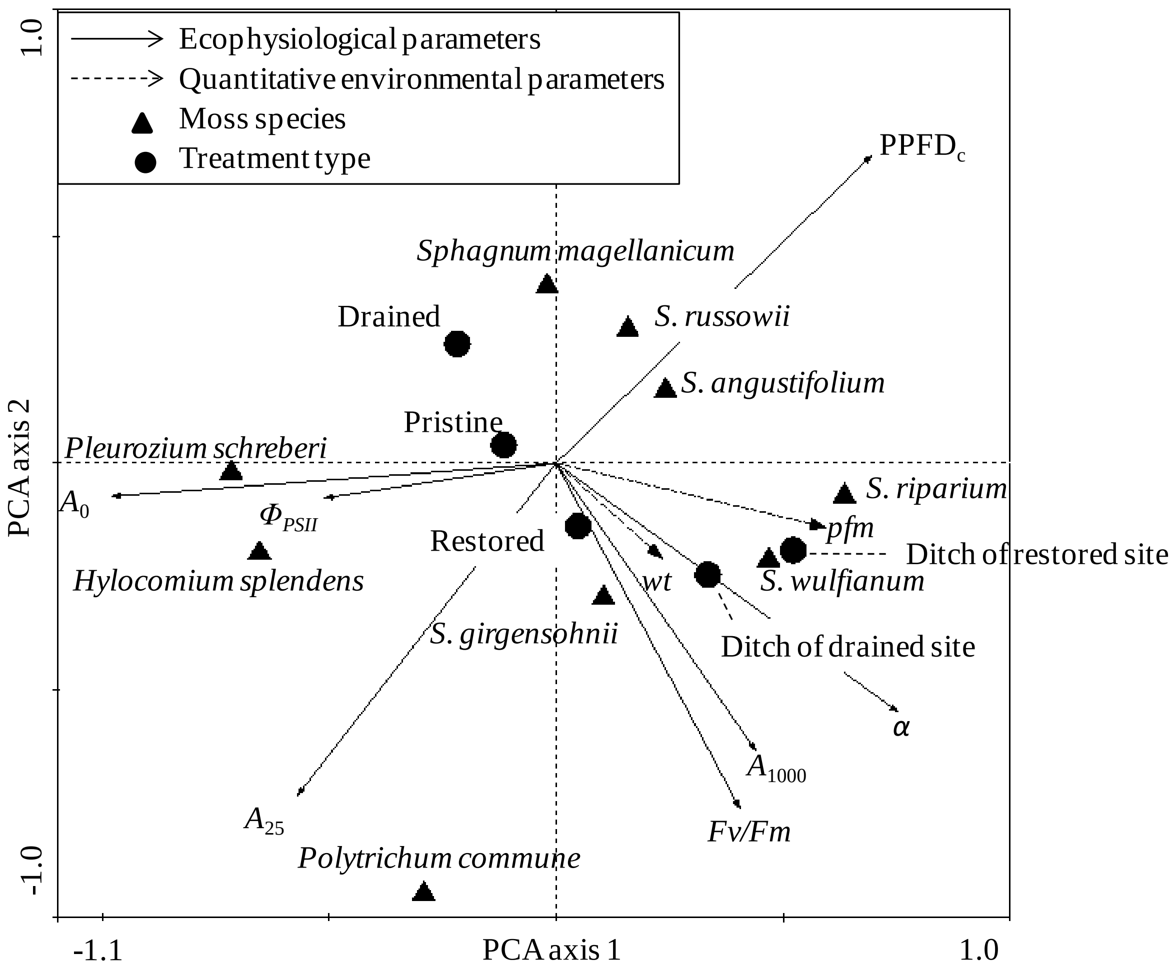


Fig. 2: Principal Component Analysis (PCA) linking ecophysiological parameters ($CO_2$ assimilation rate at three levels of PPFD ($A_{1000}$, $A_{25}$, and $A_0$), maximum quantum yield of $CO_2$ assimilation ($\alpha$), light compensation point of $A$ (PPFD$_c$), and maximum and apparent quantum yield of PSII ($F_v/F_m$ and $\Phi_{PSII}$)) with environmental parameters (moss species, treatment type, site water table (*wt*), and peat field moisture (*pfm*)) during May. Both treatment type and *Sphagnum* species formed a linear gradient according to potential photosynthesis ($A_{1000}$) and stress level, indicated by $\alpha$ and $F_v/F_m$. Species in wetter environments and treatments characterized by high water levels had the highest rate of potential photosynthesis ($A_{1000}$) and lower stress.

## DISCUSSION

While the effect of species explained the greatest amount of ecophysiological variation, the treatment type can have a strong effect on the species composition. Following drainage, *Sphagnum* cover typically decreases in area and is largely replaced by forest mosses (Laine *et al.,* 1995). Forest mosses are typically slow growing and tolerant of shade, as evidenced in this study by the low carbon assimilation rates and lower light compensation points of the forest mosses *Pleurozium schreberi* and *Hylocomium splendens*. While conditions are poor for *Sphagnum* growth in drained mires, drainage ditches offer a refuge for *Sphagnum* species to persist. During May, *Sphagnum* mosses in the ditches of drained sites exhibited high potential photosynthesis, similar to ditches in restored sites.

Following restoration, the higher water table enables *Sphagnum* cover to expand in area, from remnant patches that persisted throughout drainage (Jauhiainen *et al.*, 2002). The high productivity measured from restored sites is typical of plant species in disturbed habitats, which are capable of quick growth to outcompete competitors. In contrast, pristine sites function more like later successional habitats with lower maximum photosynthesis rates and light saturation at lower light intensities (Bazzaz, 1979, Laine *et al.*, 2011). These different growth conditions resulted in treatments being distinguished between wet and disturbed sites (restored) and drier, more stabilized sites (pristine and drained).

While restored sites are still quite different from pristine sites on an ecophysiological basis, the high productivity rates will enable a faster rate of peat depostition and accumulation. Longer term studies will be useful to determine how long it takes for *Sphagnum* mosses in restored spruce mires to begin functioning ecophysiologically similar to mosses in pristine mires.

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