

Surface energy exchange in pristine and managed boreal peatlands

P. Alekseychik¹, I. Mammarella¹, A. Lindroth², A. Lohila⁴, M. Aurela⁴, T. Laurila⁴, V. Kasurinen⁸, M. Lund⁷, J. Rinne², M.B. Nilsson³, M. Peichl³, K. Minkkinen⁸, N.J. Shurpali⁵, E.-S. Tuittila⁶, P.J. Martikainen⁵, J.-P. Tuovinen⁴ and T. Vesala^{1,8}

¹Institute for Atmospheric and Earth System Research (INAR) / Physics, University of Helsinki, Finland

²Department of Physical Geography and Ecosystems Science, Lund University, Sweden

³Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, Umeå, Sweden

⁴Finnish Meteorological Institute, Climate System Research, Helsinki, Finland

⁵Department of Environmental and Biological Sciences, University of Eastern Finland, Kuopio campus, Finland

⁶School of Forest Sciences, University of Eastern Finland, Joensuu, Finland

⁷Department of Bioscience, Arctic Research Centre, Aarhus University, Roskilde, Denmark

⁸Institute for Atmospheric and Earth System Research (INAR) / Forest Sciences, University of Helsinki, Finland

SUMMARY

Surface–atmosphere energy exchange is strongly ecosystem-specific. At the same time, as the energy balance constitutes responses of an ecosystem to environmental stressors including precipitation, humidity and solar radiation, it results in feedbacks of potential importance for the regional climate. Northern peatlands represent a diverse class of ecosystems that cover nearly 6×10^6 km² in the Boreal region, which makes the inter-comparison of their energy balances an important objective. With this in mind we studied energy exchange across a broad spectrum of peatlands from pristine fens and bogs to forested and agriculturally managed peatlands, which represent a large fraction of the landscape in Finland and Sweden. The effects of management activities on the energy balance were extensively examined from the micrometeorological point of view, using eddy covariance data from eight sites in these two countries (56° 12'–62° 11' N, 13° 03'–30° 05' E). It appears that the surface energy balance varies widely amongst the different peatland types. Generally, energy exchange features including the Bowen ratio, surface conductance, coupling to the atmosphere, responses to water table fluctuations and vapour pressure deficit could be associated directly with the peatland type. The relative constancy of the Bowen ratio in natural open mires contrasted with its variation in tree-covered and agricultural peatlands. We conclude that the impacts of management and the consequences of land-use change in peatlands for the local and regional climate might be substantial.

KEY WORDS: Bowen ratio, land use, peatland management, surface energy balance

INTRODUCTION

Boreal and Arctic ecosystems play a significant role in regional and global climate (Chapin *et al.* 2000). Surface energy exchange is an important ecosystem–climate feedback process and the peatland energy balance is a primary determinant of the local, regional and global climate, in addition to greenhouse gas budgets (Eugster *et al.* 2000). Net radiation (R_n) determines the amount of energy available for conversion into sensible (H) or latent (LE) heat fluxes and heat storage (S) in an ecosystem, while vegetation and soil properties strongly affect the partitioning between latent and sensible heat (Bonan *et al.* 2002, Betts *et al.* 2007). These aspects, along with weather patterns (Harazono *et al.* 1998), link ecosystem energy balance to regional and global climate.

Boreal ecosystems exhibit a wide spectrum of energy balances due to their differences in vegetation cover, hydrology, soil type and occurrence of open water surfaces (*e.g.* Beringer *et al.* 2005, Eugster *et al.* 2000, Betts *et al.* 2007, Lafleur 2008, Kasurinen *et al.* 2014 and others). In the boreal land cover mosaic, a significant fraction of the total land area is represented by peatlands (30 % in Finland and 15 % in Sweden), a particularly diverse class of fen and bog ecosystems defined by the presence of organic soil (*e.g.* Bridgham *et al.* 1999). Globally, boreal peatlands occupy more than 5.8×10^6 km² of the Earth's surface in Canada, USA, Fennoscandia and Russia (Bleuten *et al.* 2006). Typically, available energy in pristine peatlands is mainly directed into latent heat flux (Kellner 2001, Shimoyama *et al.* 2003, Wu *et al.* 2010 and the review in Runkle *et al.* 2014). These ecosystems also show substantial

resilience to hydrological changes (Beleya & Baird 2006, Waddington *et al.* 2015).

A few studies of the boreal peatland energy balance (*e.g.* Bridgham *et al.* 1999, Kurbatova *et al.* 2002, Beringer *et al.* 2005, Lafleur *et al.* 2005, Peichl *et al.* 2013, Runkle *et al.* 2014 and others) have focused on pristine unmanaged mires, and identified two major features, outlined below.

- First, the energy balance is largely a product of waterlogged conditions (*e.g.* Bridgham *et al.* 1999) leading to latent heat fluxes equal to or greater than sensible heat fluxes (*e.g.* Bay 1968, Kurbatova *et al.* 2002, Sottocornola & Kiely 2010, Peichl *et al.* 2013, Runkle *et al.* 2014). The thermal capacity and conductivity of water-saturated peat lead also to significant soil heat storage. The water table depth (*WT*) and the bulk surface (stomatal) conductance are coupled (*e.g.* Kurbatova *et al.* 2002, Raddatz *et al.* 2009, Sottocornola & Kiely 2010), especially when the cover of vascular plants is continuous (*e.g.* Acreman *et al.* 2003, Peichl *et al.* 2013). Phenology of the dominant vegetation is a major controller of energy exchange (*e.g.* Burba *et al.* 1999, Shurpali *et al.* 2013, Kasurinen *et al.* 2014), operating through the link between water vapour pressure deficit (*VPD*) and stomatal conductance (*e.g.* Liljedahl *et al.* 2011, Peichl *et al.* 2013) as well as through variations in plant albedo (Waddington *et al.* 2015).
- Secondly, moss cover plays a major role in ecosystem-scale evapotranspiration (*ET*) (*e.g.* Liljedahl *et al.* 2011). Mosses are sensitive to drying (Gerdol *et al.* 1996), although moss species have become adapted to a wide range of water levels (Hayward & Clymo 1982). In open pristine peatlands with continuous moss cover, the state of the moss layer determines a number of important ecosystem-scale parameters such as the Bowen ratio and the ratio of actual to potential evapotranspiration (Price 1991). Even at sites where vascular plant (sedge) cover is substantial, the moss layer is still the main source of *ET*, as in an Alaskan tundra site studied by Liljedahl *et al.* (2011). Nevertheless, bulk surface conductance in moss-dominated communities remains a strong function of *VPD* (Liljedahl *et al.* 2011, Peichl *et al.* 2013).

However, these features of pristine mires are largely eliminated by peatland management. In the Fennoscandian region, only about 50 % of the original peatland area has remained in its pristine state to this day. Boreal peatlands have experienced extensive human influences including drainage for

the establishment of crop plantations, afforestation or peat extraction for fuel (*e.g.* Lohila *et al.* 2004, Lohila *et al.* 2007, Shurpali *et al.* 2009, Maljanen *et al.* 2010, Järveoja *et al.* 2016). Finland and Sweden together have 45 % of the world's forestry-drained peatlands (Minkkinen *et al.* 2008). Conversion to agriculture has so far affected about 10 % of the combined Finnish and Swedish peatland area (Maljanen *et al.* 2010). It is recognised that lowering the water table in peatlands seems to modify the greenhouse gas balance by leading to reduced CH₄ emissions but increased CO₂ and N₂O emissions (Lohila *et al.* 2004, Desjardins *et al.* 2007, Lohila *et al.* 2007, Shurpali *et al.* 2009, Maljanen *et al.* 2010, Lohila *et al.* 2011, Ojanen *et al.* 2012, Ojanen *et al.* 2013, Petrescu *et al.* 2015). However, large-scale peatland management activities have also inadvertently affected the ecosystem energy balances. As a result of different measures - drainage, peat extraction and establishment of forests or croplands - all the main ecosystem features that are relevant for the surface energy balance become altered. This affects partitioning and seasonality of the surface energy fluxes, which feeds back to climate. Afforestation of a peatland, whether natural or anthropic, entails a transition to a new energy balance (Lohila *et al.* 2004, Lohila *et al.* 2007); boreal forests have a lower albedo and tighter biological control on surface conductance (*e.g.* Launiainen 2010). Conversely, crop cultivation leads to high evapotranspiration and turns crop phenology and agricultural practices into important controllers of surface energy exchange (Lohila *et al.* 2004, Shurpali *et al.* 2009, Shurpali *et al.* 2013).

As one can see, the *corpus* of previous studies clearly outlines the importance of the boreal peatland energy balance, its characteristic features and sensitivity to management. These considerations lead to the main hypothesis of this study: the peatland class - from pristine peatland to forest-covered or agricultural - is the major determinant of the surface energy balance and governs the responses to environmental drivers over a broad range of temporal scales. Correspondingly, we expect to see substantially different energy balance responses to the main environmental drivers. To test these hypotheses, we determine the differences between peatland classes in their responses to changing water availability and in the seasonality of energy exchange processes. We examine 43 site years of eddy covariance (*EC*) and auxiliary data from eight sites representing a gradient from pristine peatland to forest-covered and agricultural land. Climatically relevant features, such as energy partitioning into sensible and latent heat fluxes and ecosystem-

atmosphere coupling, are investigated. Finally, we analyse how the peatlands can be classified according to mean values of ecophysiological and micrometeorological parameters controlling energy exchange.

METHODS

Energy balance

The overall surface energy balance was expressed as:

$$R_n - G - S_H - S_{LE} - S_{bio} = H + LE \quad [1]$$

where R_n is net radiation, G is the soil heat flux, S_H the sensible heat storage in the air, S_{LE} the storage of latent heat and S_{bio} the heat storage in biomass.

The sensible and latent heat storage change fluxes were calculated from the changes in air temperature (T_a) and water vapour content of the air column (*e.g.* Haverd *et al.* 2007):

$$S_H = \int_0^{z_{EC}} \rho C_p \frac{dT_a}{dt} dz \approx \sum_{i=1}^n \left(\rho C_p \frac{\Delta T_a}{\Delta t} \Delta z_i \right) \quad [2]$$

$$S_{LE} = \int_0^{z_{EC}} \rho \Lambda \frac{d\chi_{H_2O}}{dt} dz \approx \sum_{i=1}^n \left(\rho \Lambda \frac{\Delta \chi_{H_2O}}{\Delta t} \Delta z_i \right) \quad [3]$$

where z_{EC} is the EC sensor mounting height (m), ρ the air density, C_p the air heat capacity at constant pressure, Λ the latent heat of vaporisation and χ_{H_2O} the atmospheric mixing ratio of water vapour (dimensionless, derived from relative humidity (RH)). Since T_a and RH were measured at only one level in each site, they had to be adopted as column averages between the ground and z_{EC} . The biomass heat storage S_{bio} was calculated using the biomass temperature T_{bio} following Launiainen (2010):

$$S_{bio} \approx M_b C_{p_{bio}} \frac{\Delta T_{bio}}{\Delta t} \quad [4]$$

where M_b is the mean biomass at the site, $C_{p_{bio}}$ the specific heat capacity of biomass and t the time. T_{bio} was obtained for the more densely forested sites (ALK, KAL, see below) as T_a with a phase shift (two hours) and 1.54 times smaller amplitude (obtained by Launiainen (2010) for the comparable SMEAR-II site, see also Hari & Kulmala (2005)). For the rest of the sites, T_{bio} was taken equal to T_a due to the smallness of the vegetation canopy's heat capacity. A biomass heat capacity value used by Lindroth *et al.* (2010), $C_{p_{bio}} = 2800 \text{ J kg}^{-1} \text{ K}^{-1}$, was adopted.

The surface ground heat flux was estimated as soil heat storage change from the temperature profiles,

integrated for the layer from soil surface to depth z following *e.g.* Ochsener *et al.* (2007):

$$G = \int_0^z C_v \frac{\partial T_p}{\partial t} dz \quad [5]$$

where C_v is the volumetric heat capacity of the soil. Finally, we defined the Bowen ratio β as the quotient of the sensible heat flux and the latent heat flux:

$$\beta = \frac{H}{LE} \quad [6]$$

Environmental and ecophysiological factors

Penman potential evapotranspiration was calculated after Penman (1948):

$$PET_P = \frac{AE\zeta + (\rho C_p VPD r_a^{-1})}{(\zeta + \gamma)\Lambda} \quad [7]$$

where the available energy (AE) equals ($R_n - G$) (other storages negligible), r_a is the aerodynamic resistance, γ the psychrometric constant and ζ the slope of the saturation vapour pressure curve. Penman-Monteith potential evapotranspiration was calculated after Monteith (1965):

$$PET_{PM} = \frac{AE\zeta + (\rho C_p VPD r_a^{-1})}{(\zeta + \gamma(1 + r_s r_a^{-1}))\Lambda} \quad [8]$$

where r_s is the bulk surface conductance. While PET_P models evapotranspiration from a fully moist surface, PET_{PM} considers an incompletely moist surface by incorporating surface resistance r_s in the expression.

Aerodynamic resistance was calculated after Verma (1989) as:

$$r_a = \frac{U}{u_*^2} + \frac{\kappa B^{-1}}{\kappa u_*} \quad [9]$$

where U is the wind speed, u_* is the friction velocity, B^{-1} is the dimensionless sublayer Stanton number (Owen & Thomson 1963) and κ is von Kármán's constant (=0.4). The values of κB^{-1} adopted were 2 for ALK and KAL (assuming they have sufficiently closed canopies, after Garratt & Hicks (1973)) and, otherwise, 3.2 (the representative value for pristine open peatlands, Mölder & Kellner (2002)).

Bulk surface resistance was derived from the Penman-Monteith equation (Thom 1975):

$$r_s = r_a \left(\frac{\zeta\beta}{\gamma} - 1 \right) + \left(\frac{\rho C_p VPD}{\gamma A E} \right) (1 + \beta) \quad [10]$$

Only daytime resistance values (9 a.m. to 3 p.m.) and periods with $R_n > 100 \text{ Wm}^{-2}$ were accepted to ensure that exclusively good-quality data were used. The aerodynamic and bulk surface conductances (g_a and g_s , respectively) are, by definition, reciprocals of the corresponding resistances: $g_a = r_a^{-1}$; $g_s = r_s^{-1}$.

A modified version of Lohammar's function was used to formalise the dependency of g_s on VPD (Oren *et al.* 1999, Launiainen 2010):

$$g_{s_mod} = g_1 - m \cdot \ln(VPD), \quad [11]$$

where g_1 is the reference conductance at $VPD = 1 \text{ kPa}$ and m is the sensitivity of g_s to VPD . g_1 and m were obtained by fitting Equation 11 to the observations.

The Ω parameter, originally proposed by Jarvis & McNaughton (1986), expresses the relative importance of the aerodynamic and surface resistances for evapotranspiration, and is often interpreted as the degree of ecosystem–atmosphere coupling. Jarvis & McNaughton (1986) define it as:

$$\Omega = \frac{\zeta / \gamma + 1}{\zeta / \gamma + 1 + g_a / g_s} \quad [12]$$

In a fully coupled state, $g_s \ll g_a$ and $\Omega = 0$. Conversely, in a maximally decoupled state, $g_s \gg g_a$ and $\Omega = 1$. In the former case, transpiration is constrained and stomatal control is the limiting factor. In the latter case, evaporation is constrained so that available energy becomes the limiting factor.

The α_{PT} parameter was originally introduced to compensate for the absence of the aerodynamic term in the Priestley-Taylor equation. It was noted that, in general, α_{PT} is inversely related to bulk surface resistance (*e.g.* Pereira 2004). α_{PT} was calculated according to the original definition by Priestley & Taylor (1972), as:

$$\alpha_{PT} = \frac{LE(\zeta + \gamma)}{(LE + H)\zeta} \quad [13]$$

Ω and α_{PT} were only accepted from the daytime period in order to avoid the complications in their definition arising at twilight and night time.

Evaporative fraction (EF) was calculated as:

$$EF = \frac{LE}{R_n} \quad [14]$$

Site descriptions

Eight measurement sites in Finland and Sweden were selected for the analysis, representing tree-covered peatlands, agricultural peatlands and pristine open mires (Figure 1, Table 1). The sites are mainly concentrated in the southern boreal region. Based on hydrology and vegetation composition, the pristine peatlands are divided into two major classes: fens, which receive nutrients from rain and groundwater and are dominated by homogeneous sedge cover; and bogs, which are rain-fed heterogeneous ecosystems with pronounced differences between ridges and hollows. Drained peatlands may have become tree-covered or be used as agricultural fields. In all cases the thickness of the peat layer after drainage and peat harvesting typically remains well over 20 cm.

Tree-covered peatlands

Alkkia (ALK), originally a natural *Sphagnum* bog, was drained in 1936–1938 and remained in agricultural use until 1969. This involved fertilisation and soil preparation by introducing a mineral soil admixture. In 1971 and 1991, the site was fertilised with phosphorus (P) and potassium (K). Pine forest with row spacing 3–8 m was established in 1971, and the mean tree height had reached 12 m by the early 2000s. Naturally growing birch now fills the spaces between the rows of pine. The measurement station is located on the boundary between the managed and natural areas, with the undisturbed peatland soils lying in the sector 135°–S–270° (Lohila *et al.* 2007). Therefore, only the data from the managed sector (270°–N–135°, 20 ha) were accepted for analysis.

Kalevansuo (KAL) was originally a tree-covered dwarf-shrub bog. It was drained in 1969, which enabled tree recovery and increased the growth of the original pine stand. During the measurements in 2005–2008, the site (~65 ha) was covered with a stand of predominantly Scots pine averaging 15 m in height, was trenched with drainage ditches at approximately 40 m intervals, and the forest floor vegetation was dominated by dwarf shrubs and *Sphagnum* mosses. The fetch of the EC system was at least 200 m in all directions (Lohila *et al.* 2011).

Agricultural peatlands

Jokioinen (JOK) has experienced about a century of agricultural exploitation. The management history includes the installation of subsurface drainage pipes in 1954 and maintenance works in 1992, when the pipes were re-buried at a greater depth of 0.8–1 m following peat subsidence in the previous years. The water table subsequently fell to around the depth of the drainage pipes. During the measurement period

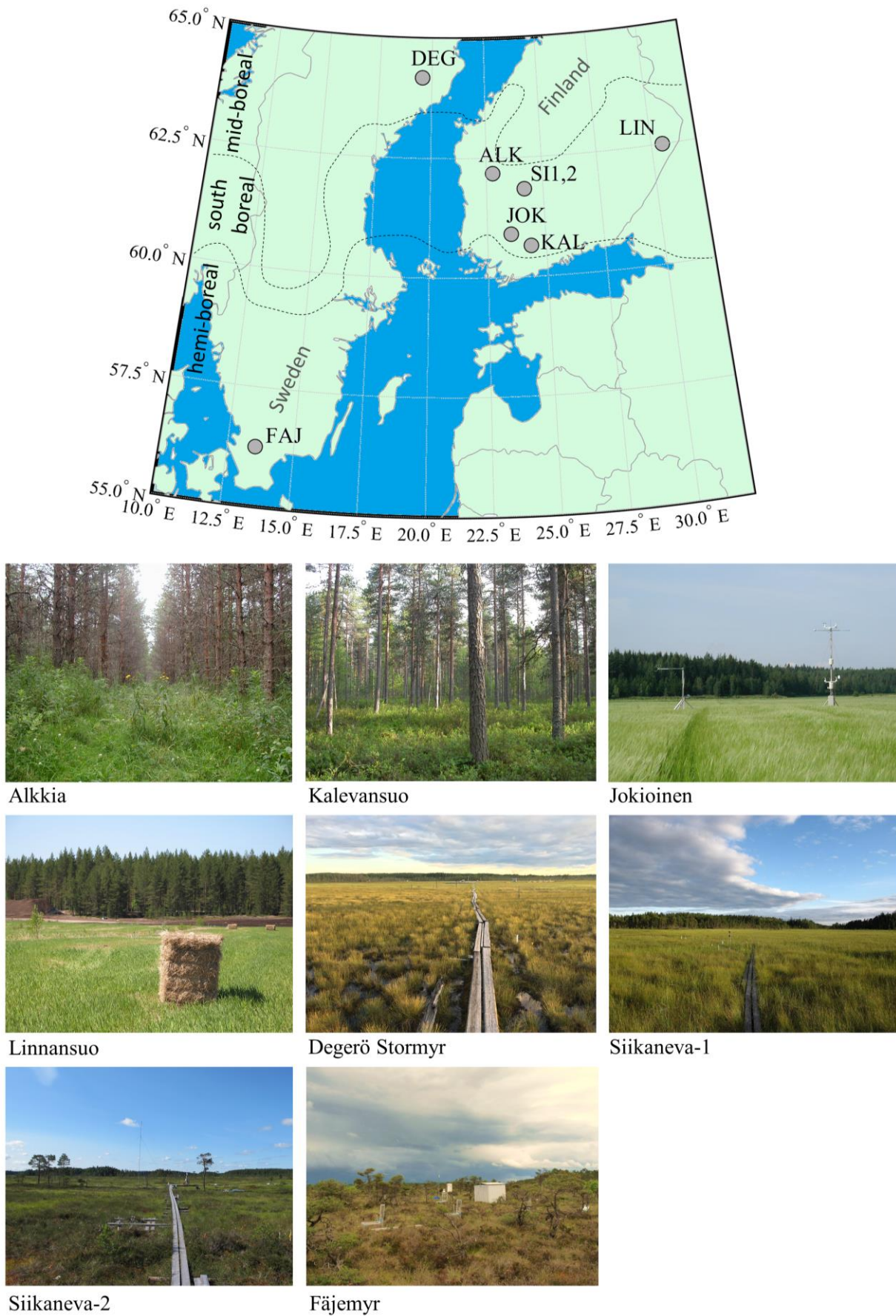


Figure 1. Above: locations of the study sites in Finland and Sweden; the boreal region zonation is based on Ahti *et al.* (1968). Below: photographs of the sites, each taken in the vicinity of the measurement setup.

Table 1. Characteristics of the measurement sites. Long-term (30–40 year) averages are given for air temperature and precipitation. Other quantities are given as growing season averages. Summer averages represent the period June–August. Negative water level values correspond to depths below moss or ground surface. The IRGA column gives the model of infrared gas analyser for water vapour concentration measurement at each site. For the key to superscripted letters, see overleaf.

Site code	Co-ords.	Period	Management status	Peat depth (m)	Water level, mean and (min/max) (cm)	Annual/summer mean T_a	Annual/summer precipitation (mm)	Aboveground biomass (kg m ⁻²); LAI (m ² m ⁻²)	IRGA	References
ALK	62.2 N 22.8 E	2002–2004	drained for agriculture, later afforested, originally bog	1.56	-48 (-56/-41)	4.1/14.8 ^a	681/232 ^a	6.40 ^b ; 4.4/2.0 ^c	LI-7000	Lohila <i>et al.</i> (2007)
KAL	60.6 N 24.3 E	2005–2008	drained for forestry, originally dwarf shrub bog	1.3–3, mean 2.2	-32 (-75/-7)	4.6/15.2 ^d	647/211 ^d	6.60 ^b ; 4.4/0.7 ^e	LI-7000	Lohila <i>et al.</i> (2011)
JOK	60.9 N 23.5 E	2000–2003	agricultural field, originally fen	0.5–0.6	-80 ^f	4.6/15.2 ^g	627/218 ^g	0.34–0.45 ^h ; 0.5–5.0 ⁱ	LI-6262	Lohila <i>et al.</i> (2004)
LIN	62.5 N 30.5 E	2004–2010	reed canary grass plantation after peat extraction, originally fen	0.2–0.85	-61 (-71/-43)	2.8/14.7 ^j	690/229 ^j	1.49 ^k ; 2.5	LI-7500	Shurpali <i>et al.</i> (2009), Shurpali <i>et al.</i> (2013)
DEG	64.2 N 19.5 E	2001–2010	pristine fen	3–4	-12 (-41/8)	1.2 ^l /13.5	523 ^l /233	0.14 ^u ; 0.8 ^m	LI-6262	Sagerfors <i>et al.</i> (2008), Peichl <i>et al.</i> (2013), Peichl <i>et al.</i> (2014)
SI1	61.8 N 24.2 E	2005–2012	pristine fen	4 ⁿ	-6 (-39/23)	3.5/14.6 ^o	711/252 ^o	0.25; 0.4 ^p	LI-7000	Rinne <i>et al.</i> (2007), Aurela <i>et al.</i> (2007), Riutta <i>et al.</i> (2007)
SI2	61.8 N 24.2 E	2011–2013	pristine bog	5–6 ⁿ	-9 (-17/7)	3.5/14.6 ^o	711/252 ^o	0.11 ^q ; 0.188 ^q	LI-7200	
FAJ	56.2 N 13.5 E	2006–2009	pristine tree-covered eccentric bog	4–5	-24 ^r (-48/-10)	6.2 ^s /15.5	700 ^s /305	0.70 ^t ; -	LI-6262	Lund <i>et al.</i> (2007), Lund <i>et al.</i> (2009)

Key to Table 1

- ^a Kankaanpää/Niinisalo meteorological station (Finnish Meteorological Institute, FMI).
^b A. Lohila, personal communication.
^c Scots pine stand two-sided leaf area index (LAI) / forest floor LAI (Launiainen *et al.* 2016).
^d Vihti/Maasoja station (Finnish Meteorological Institute, FMI).
^e Scots pine stand two-sided LAI / forest floor LAI (Launiainen *et al.* 2016).
^f an estimate based on the depth of the drainage pipes, A. Lohila, personal communication.
^g Jokioinen observatory (Finnish Meteorological Institute, FMI).
^h mean values for forage grass and barley, respectively.
ⁱ typical range in summer; rapid crop growth and varying harvest times create much variation (Lohila *et al.* 2004).
^j Tohmajärvi/Kemie station (Finnish Meteorological Institute, FMI).
^k mean value of the intermediate-wetness plots (Shurpali *et al.* 2013).
^l Alexandersson *et al.* (1991).
^m summer peak total LAI, M. Peichl, personal communication and Peichl *et al.* (2015).
ⁿ P. Mathijssen, personal communication.
^o Drebs *et al.* (2002).
^p one-sided LAI (Riutta *et al.* 2007).
^q A. Korrensalo, personal communication.
^r May–September mean value. The original *WT* values were corrected by adding -20 cm for better representativeness of the mean *WT* within the EC footprint (M. Lund, personal communication).
^s meteorological station of the Swedish Meteorological and Hydrological Institute.
^t approximate value (M. Lund, personal communication).
^u Laine *et al.* (2012).

(2000–2003), barley and forage grass were alternately cultivated at the site (Lohila *et al.* 2004).

Linnansuo (LIN) is located in eastern Finland. After initial drainage, peat extraction for fuel was carried out at Linnansuo between 1976 and 2001. By the time peat extraction ceased, the remaining peat layer was only 20–85 cm deep. Subsequently, the site was fertilised with nitrogen (N), phosphorus (P) and potassium (K) and used as an experimental plantation of “Palaton” reed canary grass (RCG). The site was also tilled once at the beginning of RCG cultivation. Later on, the site was fertilised every year at the rates recommended for regional farming (N applications of about 60 kg ha⁻¹). After the third year following planting, RCG was harvested every year. The mean peak height of the bioenergy crop was 1.7 m in the years 2004–2010 (Shurpali *et al.* 2009).

Pristine fens

Degerö Stormyr (DEG) is an acidic mire system covering 6.5 km², located in the county of Västerbotten, Northern Sweden. The mire complex comprises multiple smaller mires separated by ridges and glacial tills. The mire surface is homogeneous, lacking pronounced microtopographical features, all around (within about 100 m of) the measurement setup. The vegetation consists of various sedge, shrub and moss species characteristic of carpet and lawn

communities (Yurova *et al.* 2007, Sagerfors *et al.* 2008, Peichl *et al.* 2013).

Siikaneva-1 (SI1) is the largest remaining pristine peatland in southern Finland. Its structure is complex and various trophic levels are represented in different areas. The first measurement site was established in the fen area of the peatland in 2004 (Aurela *et al.* 2007, Rinne *et al.* 2007). The distribution of microforms is rather uniform within at least 200 m around the measurement station; microtopographical features, such as strings/hollows, are sparse in that vicinity. The vegetation is dominated by typical peatland mosses (*Sphagnum rubellum*, *Sphagnum papillosum*, *Sphagnum fuscum*) and vascular species (*Rhynchospora alba*, *Andromeda polifolia*) (Rinne *et al.* 2007, Riutta *et al.* 2007, Korrensalo *et al.* 2017).

Pristine bogs

Siikaneva-2 (SI2) is a new station, established in 2011 just 1.2 km NW of Siikaneva-1. Despite the close proximity to the fen ecosystem of Siikaneva-1, Siikaneva-2 is a bog. Typical bog features, such as a greater amplitude of microtopographical (hollow-hummock) variation and a denser cover of shrubs, set Siikaneva-2 apart from Siikaneva-1. Also characteristic are the ‘mud bottoms’ - patches of peat completely devoid of moss with only very sparse sedge cover. Small, isolated Scots pine trees populate

the strings, but the tree density is lower than on Fäjemyr.

Fäjemyr (FAJ) in southern Sweden is a pristine, well-developed eccentric bog (raised bog with an asymmetric dome, Seppä 2002). Therefore, the water table is relatively low compared with the other pristine peatlands in this study. So far, the only external influence in the area has been the deposition of N of anthropic origin. The site features a well-developed microtopography of hummocks, carpets and lawns, while hollows are less common (Lund *et al.* 2007). The site is vegetated with a mixture of dwarf shrubs, *Sphagnum* mosses and sedges, with a sparse tree cover formed by dwarf pine.

Measurements

All of the sites were equipped for measurement of each energy balance component. Net radiation sensors and eddy-covariance setups provided latent and sensible heat flux data. Auxiliary measurements included T_a and RH, T_p profiles at 3–8 depths, precipitation intensity, water table depth and wind

data (wind speed, wind direction (WD) and friction velocity). The time resolution of all measurements was 30 minutes. Local solar time is used to ensure that the energy flux time series from all sites are in phase. Details of instrumentation and raw data treatment are provided in the publications listed in Table 1, and the micrometeorological characteristics of the sites are given in Table 2. The energy balance closure was 66–110 % (Table 2), which is within the typical range given by Wilson *et al.* (2002a, 2002b). Energy balance closure was calculated as a quotient of cumulative sums, $(LE+H)/(R_n-S)$. Reasons for the imbalance in energy closure are still under debate (Foken 2008), but there is a tendency for both latent and sensible heat fluxes to be affected in the same proportion (Wilson *et al.* 2002b).

Volumetric water content profile $\theta(z)$ was modelled as a function of water level (Weiss *et al.* 1998, Yurova *et al.* 2007):

$$\theta(z) = \phi[1 + (a(-(WT - z)))^b]^{-1+1/b} \quad [15]$$

Table 2. EC metadata and auxiliary information including the sensor mounting height, quality criteria (accepted WD and u_* threshold), the coverage of quality-checked and filtered EC data for the growing season and energy balance closure estimates.

Site code	EC height (m)	Accepted WD (°)	u_* threshold (m s^{-1})	EC data coverage (%)	Energy balance closure (%)
ALK	18.0	270–N–135	0.2 ^a	30	110
KAL	17.5/21.5	all	0.1 ^b	69	101
LIN	3.7	140–S–310	0.1 ^c	30	80
JOK	3.0	all	0.1 ^d	56	60
DEG	1.8	all	0.1 ^e	80	101
FAJ	3.4	all	0.1 ^f	82	66
SI1	2.5	50–S–280	0.1 ^g	65	92
SI2	2.5	100–S–340	0.085 ^h	36	74

^a Lohila *et al.* (2007).

^b Lohila *et al.* (2011).

^c Shurpali *et al.* (2009).

^d Lohila *et al.* (2004).

^e no u_* -filtering was applied in the earlier publications of DEG data, but due to the similarity of the surface roughness we chose to use the same u_* -threshold as for the other treeless sites in this study.

^f Lund *et al.* (2007).

^g a threshold of 0.2 m s^{-1} was used in a carbon budget study by Rinne *et al.* (2007); however, a 0.1 m s^{-1} threshold is used in this study.

^h visually determined from the relationship between nocturnal respiration and u_* .

Porosity (ϕ) was assumed to be equal to 95 % (average of the representative values for acrotelm and catotelm, Granberg *et al.* 1999), while values for the empirical parameters a and b were adopted from Yurova *et al.* (2007). Therefore, the volume fraction of solid peat particles constituted the remaining 5 %. The total volumetric heat capacity was then calculated as the sum of the volumetric heat capacities of solid, water and air constituents, weighted by their volume fractions in the soil matrix. The soil heat flux calculated using this estimate for moisture profile closely approached the storage-corrected heat plate flux (not shown). However, since the latter was only available for LIN, for consistency we derived G from the peat temperature profile at each site (Equation 5).

Flux data quality screening and gap-filling

Only the growing season (May–October) data were selected for the analyses, with coverage of 30–82 % after quality control. Based on the observation of energy balance closure saturation as a function of u^* with a threshold of 0.1–0.2 m s^{-1} (not shown) we excluded the low- u^* EC data, which resulted in removal of 6–25 % of the data. Additionally, in four sites the EC fluxes were only accepted from within certain wind sectors in order to avoid the effects of flow distortion due to the presence of the mast or unrepresentative areas within the EC footprint (see Table 2). At each site except LIN, the H_2O analysers providing the LE data were of the closed-path design that is insensitive to precipitation and has fewer

associated uncertainties than the other analyser types (Haslwanter *et al.* 2009). All EC data were analysed following state-of-the-art postprocessing methods (Aubinet *et al.* 2012).

The daytime LE and H were gapfilled with the model values estimated from linear regressions against R_n constructed in a moving time window of 30 days. The R_n range available within a time window was divided into four equal-sized bins and linear fitting was performed on the corresponding bin averages, generating reliable linear regressions of LE and H versus R_n . The night-time fluxes were gapfilled with the mean good-quality nocturnal flux value in the moving window, as it proved difficult to formulate a more detailed statistical model of nocturnal energy exchange. When R_n was not available for a particular 30-minute period and/or fitting was not feasible due to lack of data, the lookup table method was used instead. In turn, R_n was gapfilled using the mean diurnal variation method and/or lookup tables, depending on data availability (*e.g.* Falge *et al.* 2001). As one can see from Table 3, an r^2 of 0.6–0.75 and an RMSE of 15–40 Wm^{-2} (50–60 for H model) were achieved. However, use of the simple modelling approach resulted in r^2 below 0.5 for LIN and JOK. The energy fluxes gapfilled with these models were used only for the calculation of growing season and multiannual averages, such as those described on page 16. For all other purposes, only the filtered and quality-controlled measurement data were used.

Table 3. r^2 and RMSE of the net radiation, latent and sensible heat flux models.

Site code	R_n model		LE model		H model	
	r^2	RMSE (Wm^{-2})	r^2	RMSE (Wm^{-2})	r^2	RMSE (Wm^{-2})
ALK	0.65	59	0.69	27	0.63	44
KAL	0.64	63	0.66	21	0.77	33
LIN	0.56	64	0.68	13	0.33	31
JOK	0.65	55	0.69	28	0.42	28
DEG	0.65	50	0.67	20	0.63	18
FAJ	0.71	52	0.81	15	0.67	14
SI1	0.66	69	0.76	23	0.72	14
SI2	0.68	61	0.77	12	0.73	31

RESULTS

Environmental conditions

All of the studied peatlands were formed under the influence of the boreal climate, which is characterised by relatively low R_n and T_a , while the naturally high water table level had been substantially altered in the managed sites. Although the geographical region covered was comparatively small, there was a degree of variation among the measurement locations in the growing season mean values of environmental drivers (Figure 2).

Seasonal variations in mean values of the main environmental drivers are shown in Figure 3. T_a and R_n values are ranked in approximate correspondence with the latitude of the site. The seasonal maximum T_a was reached in July–August, while the most intense sunshine occurred in May–July. VPD also peaked in June–July, with highest summertime means between 0.4 and 0.6 kPa in different sites. However, one variable that is more a consequence of the ecological background and management history, the water table position, showed site-dependent mean values and seasonality. WT varied between the peat surface and -30 cm in the pristine peatlands, while the

variation was typically between -20 and -50 cm in the forested peatlands and -60 to -80 cm in the peatland crop plantations. A common feature was the summertime drawdown of WT in the sites with high mean WT , starting after snowmelt and continuing until late August. In contrast, ALK, JOK and LIN had seasonally more stable WT .

Diurnal course of energy balance components

The maximum daily values of LE clearly differed between the sites (Figure 4a). The maximum midday LE varied from 64 Wm^{-2} (JOK) to 127–134 Wm^{-2} (LIN, ALK). The mean diurnal variations in the remaining sites were contained between these lower and upper envelopes. The highest mean diurnal maximum of H was observed at KAL (151 Wm^{-2}) and the lowest at SI2 (50 Wm^{-2} ; Figure 4b). At three sites (ALK, KAL, FAJ), H was clearly higher than in the rest of the studied peatlands. H was typically negative at night, with nocturnal values averaging -5 Wm^{-2} (SI2) to -19 Wm^{-2} (ALK). The hourly mean maxima of R_n reached 189 Wm^{-2} at the northernmost site DEG and 296 Wm^{-2} at FAJ; the nocturnal minima of R_n ranged from about -11 to -43 Wm^{-2} (FAJ and SI2, respectively, Figure 4c).

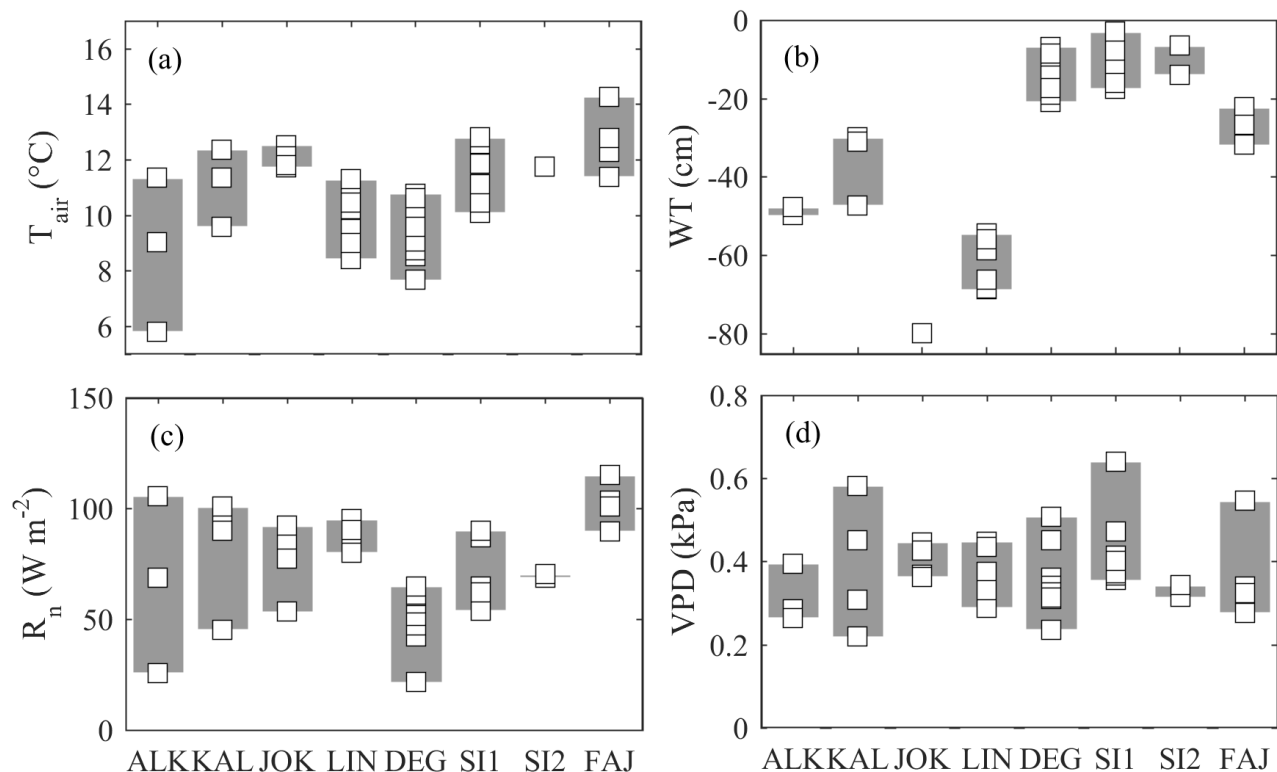


Figure 2. Mean growing season values of (a) air temperature, (b) water table level, (c) net radiation and (d) vapour pressure deficit for individual years. The grey bars show the interannual range.

G followed R_n (Figure 4c, d) with a lag of 1–3 hours that resulted mainly from the absence of temperature sensors in the uppermost 2–5 cm of soil. Nonetheless, the overall losses in the ground surface heat flux were probably not large, as the temperature at the shallowest measurement depth was assigned to the soil layer from topsoil to midway between the top and second-from-top temperature sensors. The amplitude of G was greatest at SI1, where it ranged between -29 and 39 W m^{-2} ; and smallest at SI2, where the variation was between -7 and 9 W m^{-2} .

The mean atmospheric storage change fluxes of sensible and latent heat and the biomass heat were small at all sites in comparison with the major energy fluxes. The highest daily mean values of S_{bio} , S_{LE} and S_H were approximately 4, 3 and 9 W m^{-2} , respectively, and were observed at the forested sites ALK and KAL. In comparison, the storage change fluxes at the other sites were 4–10 times smaller (Figure 4e, f, g).

Seasonality of energy partitioning

The three open mires with high water level (DEG, SI1, SI2) showed nearly constant summertime Bowen ratio (Figure 5a), whereas the hemi-boreal bog FAJ and the four managed sites displayed a wider seasonal amplitude of β . The sites KAL and FAJ were the driest, as their monthly β started at 2 or above in spring and then fell off rapidly to a minimum of 1–1.5 by mid-summer. In contrast, β in the ‘wetter’ open mires DEG, SI1 and SI2 remained rather constant at about 0.5 between May and September. These variations in energy partitioning were augmented, in part, by the well-pronounced seasonal course of net radiation. In the majority of sites, R_n reached its annual peak in May; however, insolation remained high until August (Figure 2c). Note also that the sensible heat flux curves formed three very consistent groups: (1) ALK, KAL and FAJ; (2) JOK and LIN; (3) SI1, DEG and SI2. In comparison, the

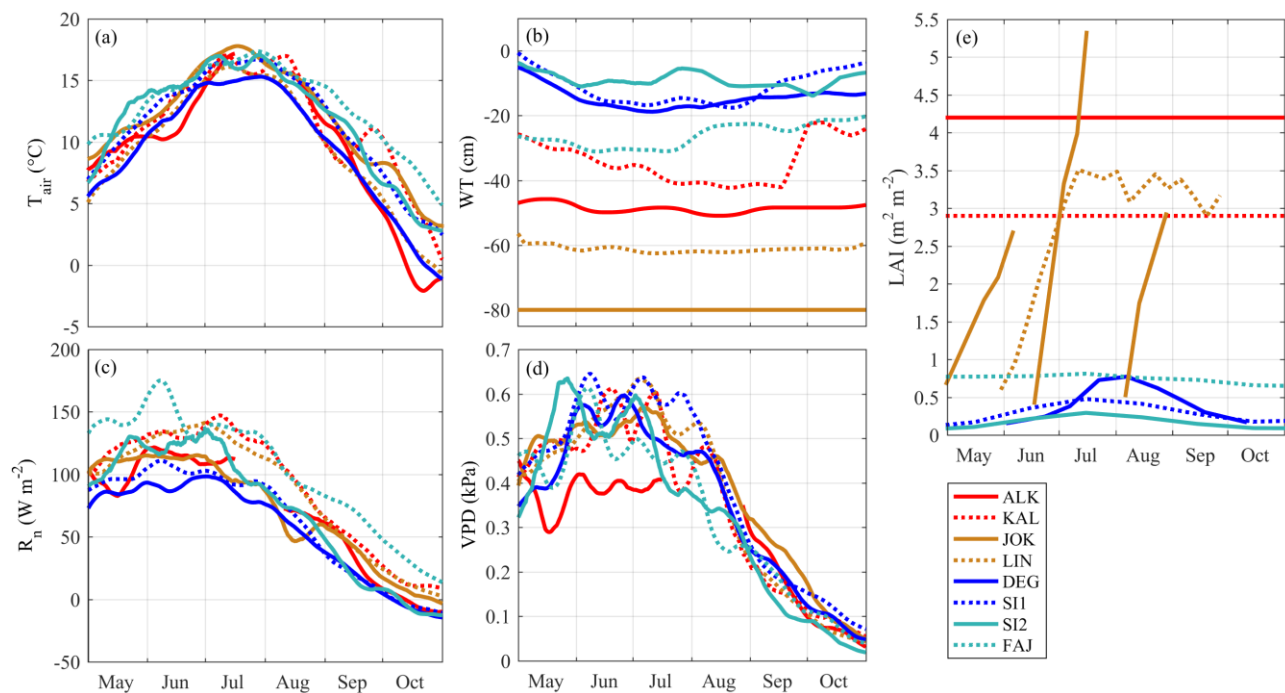


Figure 3. Mean seasonal courses of the main driving factors; (a) air temperature, (b) water table position, (c) net radiation, (d) vapour pressure deficit and (e) total leaf area index (LAI). The curves represent 7-day moving averages. Constant WT is shown for JOK, which lacked continuous observations; WT at ALK is an interpolant of monthly measurements. Colour-coding corresponds to the peatland site classes (treed in red, croplands in brown, pristine fens in blue and pristine bogs in cyan). LAI of ALK and KAL are adopted from Launiainen *et al.* 2016; LAI of Jokioinen is the 2002 measurement (forage grass), adopted from Lohila *et al.* 2004; LIN LAI is the 2007–2010 average course from Shurpali *et al.* 2013; DEG LAI is the 2012 measurement (Peichl *et al.* 2015); SI1 and SI2 LAI are the averages of 4–5 years (Alekseychik *et al.* 2017); FAJ LAI was modelled using the modified relationship between LAI and roughness length observed in SI2 (Alekseychik *et al.* 2017).

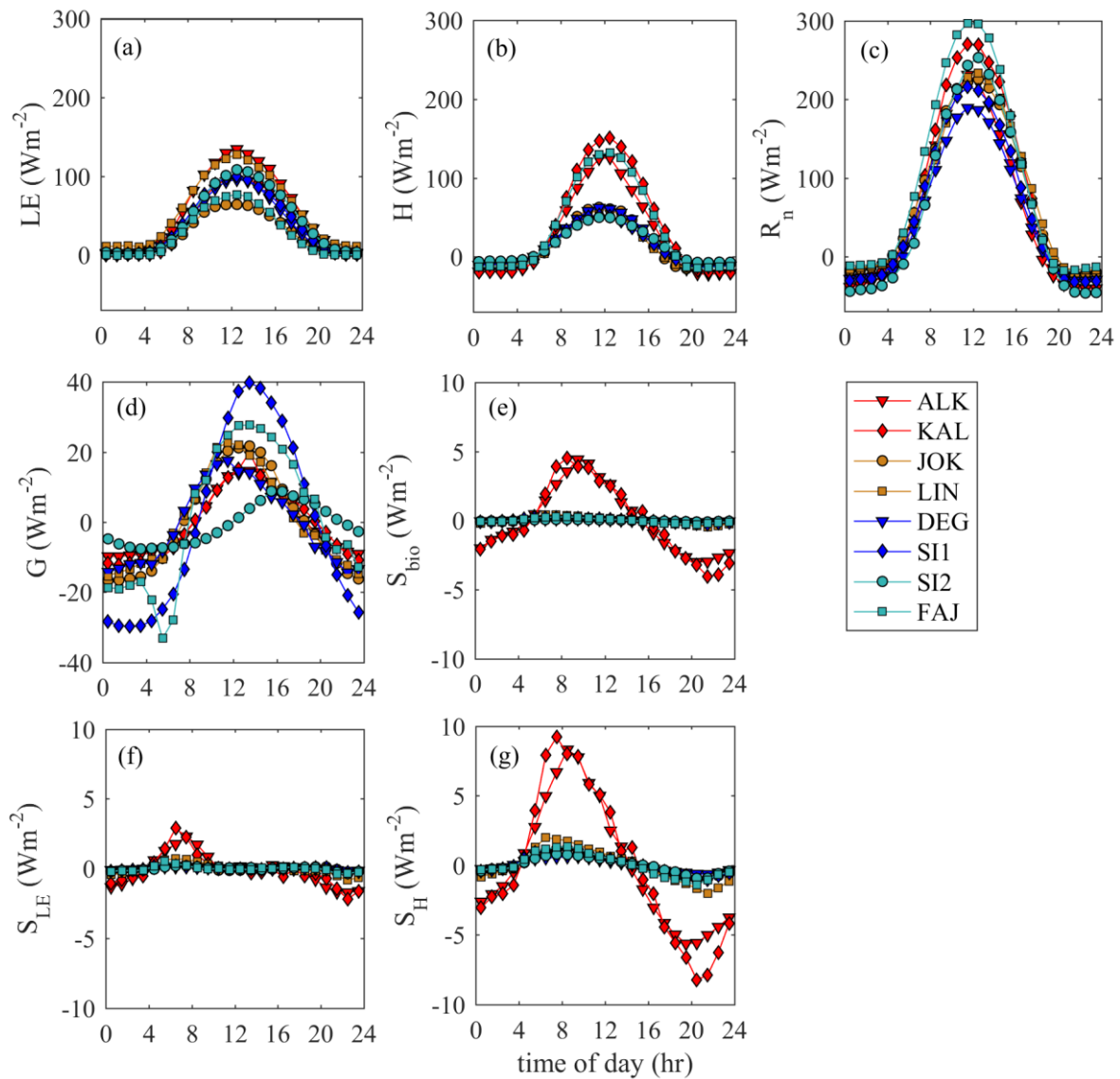


Figure 4. Mean growing season diurnal courses of (a) LE , (b) H , (c) R_n , (d) G , (e) S_{bio} , (f) S_{LE} , (g) S_H . Colour coding as in Figure 3.

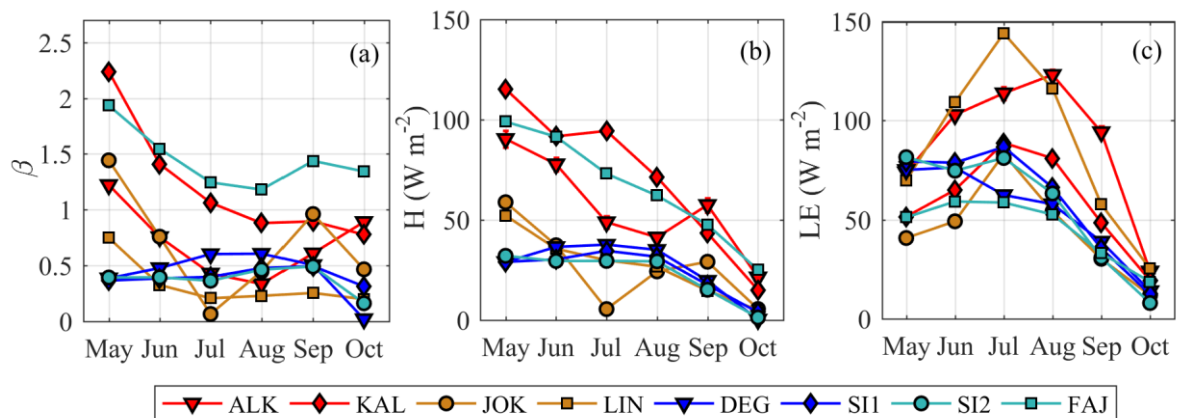


Figure 5. Growing season Bowen ratio (a, calculated as the quotient of cumulative H and LE) and monthly averages of observed sensible (b) and latent (c) heat fluxes. β is the quotient of cumulative H and LE in the respective months. The bars showing standard deviation of the mean are mostly hidden behind the markers. Colour coding as in Figure 3.

latent heat flux seasonal curves did not demonstrate clear grouping.

Evapotranspiration as a function of environmental drivers and management status

Water availability, in both air and soil, is an important factor for peatland ecology and the derivative features characterising surface energy exchange. In order to address this link, the effect of variation in the amount of moisture supply on evapotranspiration and the coupling with the atmosphere in different peatland types were investigated. The first factor, surface conductance, is presented in Figure 6 as a function of vapour pressure deficit (*VPD*). The typical range of *VPD* occurring in the data, up to 3 kPa, is shown. The absolute majority of the g_s 30-minute average data were under 60 mm s^{-1} , although the g_s range was very site-dependent. A logarithmic relationship between *VPD* and g_s , characterised by rapid reduction in g_s as *VPD* increased from 0 to 1 and an asymptotic behaviour at higher *VPD*, was observed at all of our sites as elsewhere (Lange *et al.* 1971, Admiral *et al.* 2006, Humphreys *et al.* 2006, Peichl *et al.* 2013 and many

others). The steepness parameter m was rather variable (2.4–9.1). In all cases, the model (Equation 11) fit to the bin averages described the observations well (RMSE range 0.4–1.5 mm s^{-1}) except at JOK, where the observed g_s changed too steeply with *VPD* to be reliably captured by the model (RMSE = 2.6 mm s^{-1}).

Another mechanism that controls evapotranspiration in peatlands is the change in water table level, a factor that is strongly affected by peatland management. This is presented as the relationships between water table position and Priestley-Taylor α , decoupling parameter, aerodynamic and bulk surface resistances in Figure 7. For ALK and JOK, the overall means of respective parameters are shown, as those sites lacked continuous *WT* measurements (monthly at ALK). In all sites, the relative importance of bulk surface resistance generally increased as the water table fell, which is suggested by both Priestley-Taylor α and decoupling parameter. α_{PT} and Ω correlated strongly with *WT* as long as it was above -25 cm (Figure 7a, b). The FAJ and SI2 curves clearly formed a common trend, implying that, although their *WT* ranges did not overlap, the

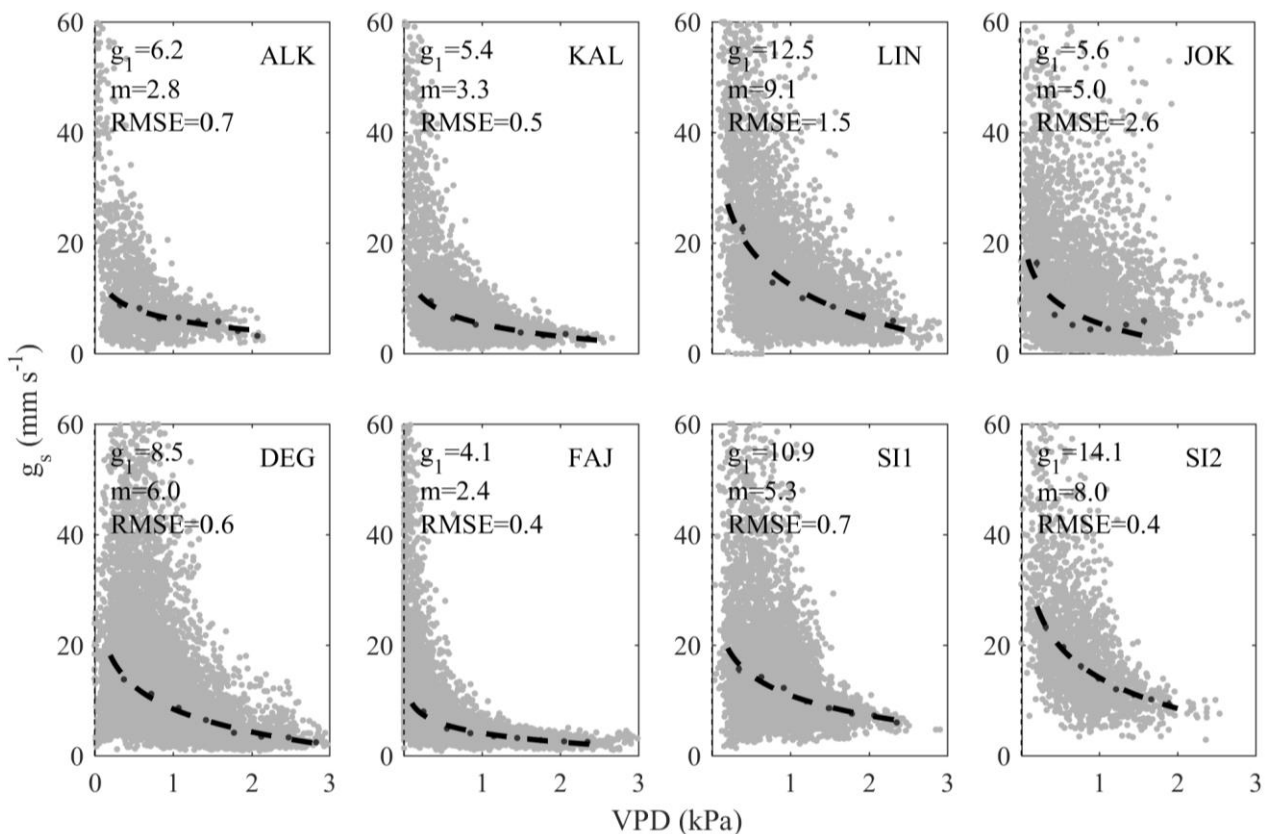


Figure 6. Dependency of bulk surface conductance on vapour pressure deficit. Grey dots show the original half-hourly data, black dots are the bin medians. The thick dashed line is the bulk surface conductance model (Equation 11) fit to the bin medians; model parameter and RMSE values are shown inside the plots.

ecosystem responses were rather similar in these two bogs. As the water table fell, vapour pressure deficit increased - very steeply in KAL and FAJ, and slower in SI1 and DEG (Figure 7c) - as did bulk surface resistance (Figure 7d, except at LIN). The above-mentioned thresholds related to the onset of ‘drought’ responses correspond to VPD around 0.5 kPa in FAJ and KAL and 0.8 kPa in DEG and SI1. Also, there was a certain upward trend in DEG, SI1, FAJ and SI2 aerodynamic conductance as a function of water level (Figure 7e). While this could not reliably be shown for SI2 with the available data, a similar relationship could be expected due to the similarity of the three pristine sites. In fact, water table dynamics were notably disparate, which points to hydrological differences between the sites. Relative temporal change in water level ΔWT was obtained by adjusting the original WT to zero at the beginning of a rainless period and then adding the observed increments until the next rainfall. What emerged was a steady, linear trend of water level change through time (Figure 8). However, the rate of water table drawdown was site-dependent: the slowest rate was at LIN (1 mm d⁻¹; mean WT = -61.2 cm) and the fastest rate was at KAL (9 mm d⁻¹; mean WT = -9.2 cm). See Figure 8 for WT

falloff rates at the other sites.

The time series of measurements shown in Figure 9 illustrate the behaviour of DEG, SI1 and FAJ over the course of three dry growing seasons. These cases were selected on the basis of no major data gaps during the driest growing seasons. All three years were characterised by scarce precipitation and elevated temperatures (not shown) which led to significant drops in WT (Figure 10a, d, g). Such weather apparently suppressed the growth of vascular plants in late summer, as g_a at DEG and SI1 peaked in June–July instead of July–August, which is more typical. The three cases have in common peaks in BR and drops in α_{PT} and g_s corresponding to the periods of moisture deficit. However, the lengths of the stress periods were not equal, being more than a month at DEG, about two weeks at SI1, and occurring as several shorter episodes at FAJ. The strength of ecosystem response correlated with the extent of dry period. The protracted drought at DEG resulted in the largest deviation in BR as it rose from the site mean of 0.45 to about 1.20 at the same time as g_s fell to unusually low levels. In contrast, SI1 showed a rather brief and modest reaction, seen as a β peak lasting for a single week in the middle of its ordinary summer

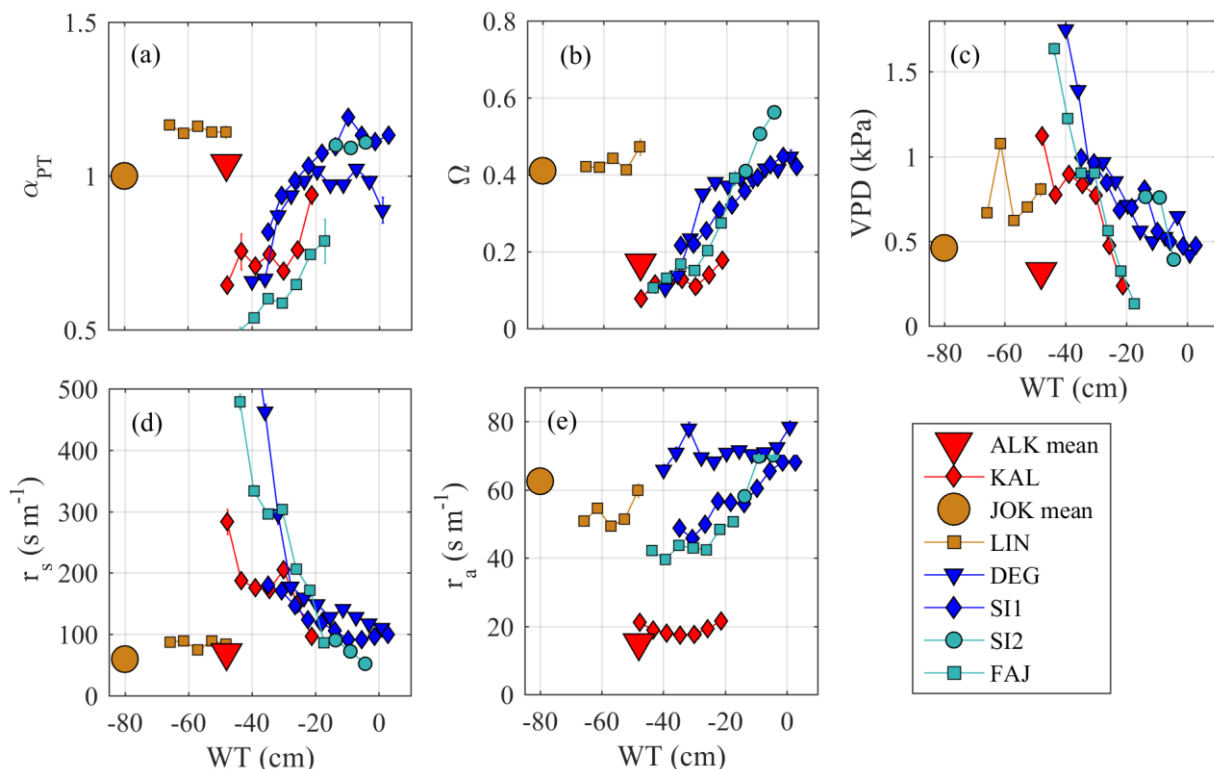


Figure 7. WT shown as a driver of (a) α_{PT} ; (b) Ω ; (c) VPD ; (d) r_s ; (e) r_a . The growing season data are averaged over WT bins. For ALK and JOK, the overall averages are shown due to data limitations. Note the unusually low α_{PT} and Ω , but high VPD and r_s at DEG when water level is around -35 cm, which is shown by data collected during a summer drought period in 2006. Colour coding as in Figure 3.

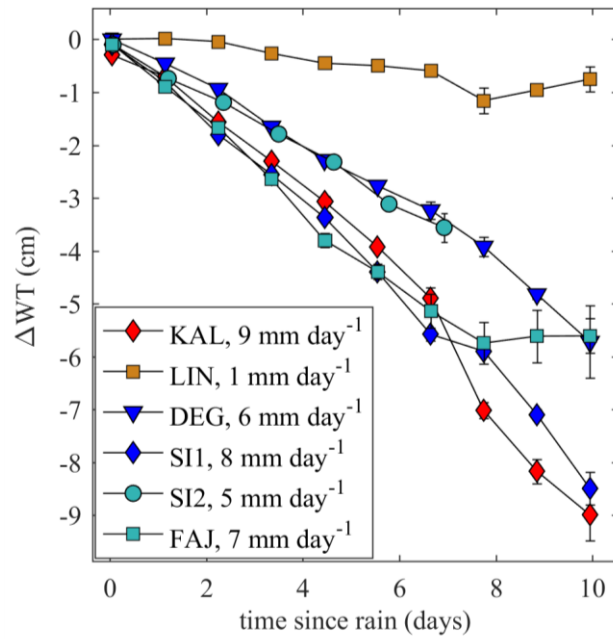


Figure 8. Change in water table position with time after rain. The symbols are bin averages for the following numbers of May–October rain events: KAL 139, LIN 294, DEG 2238, SI1 1544, SI2 651 and FAJ 2118. The WT falloff rates are specified in the legend. Error bars indicate the STD of the mean; colour coding as in Figure 3.

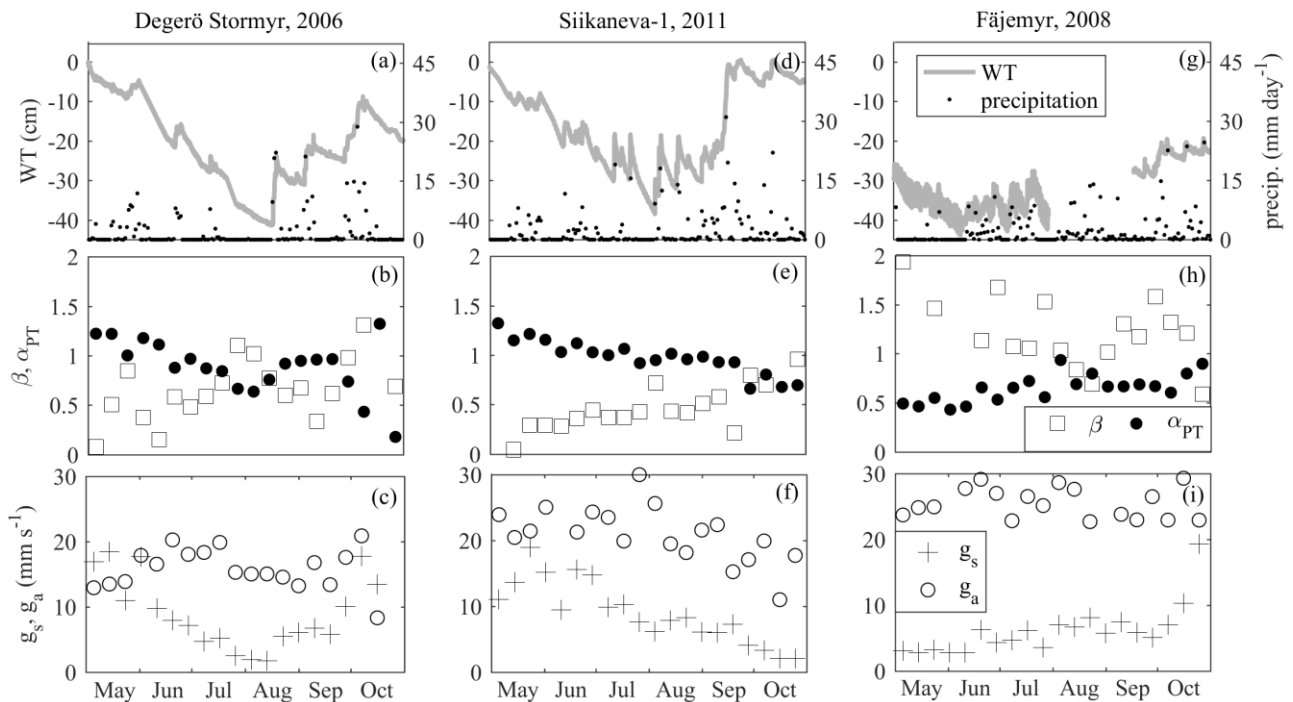


Figure 9. Case studies of three dry years at DEG (2006, a–c), SI1 (2011, d–f), and FAJ (2008, g–i). The panels show the growing-season time series of water table, precipitation, Bowen ratio, Priestley-Taylor alpha, surface and aerodynamic resistances. WT is shown as 30-minute averages and precipitation as daily sums, while the markers in the other panels represent weekly medians.

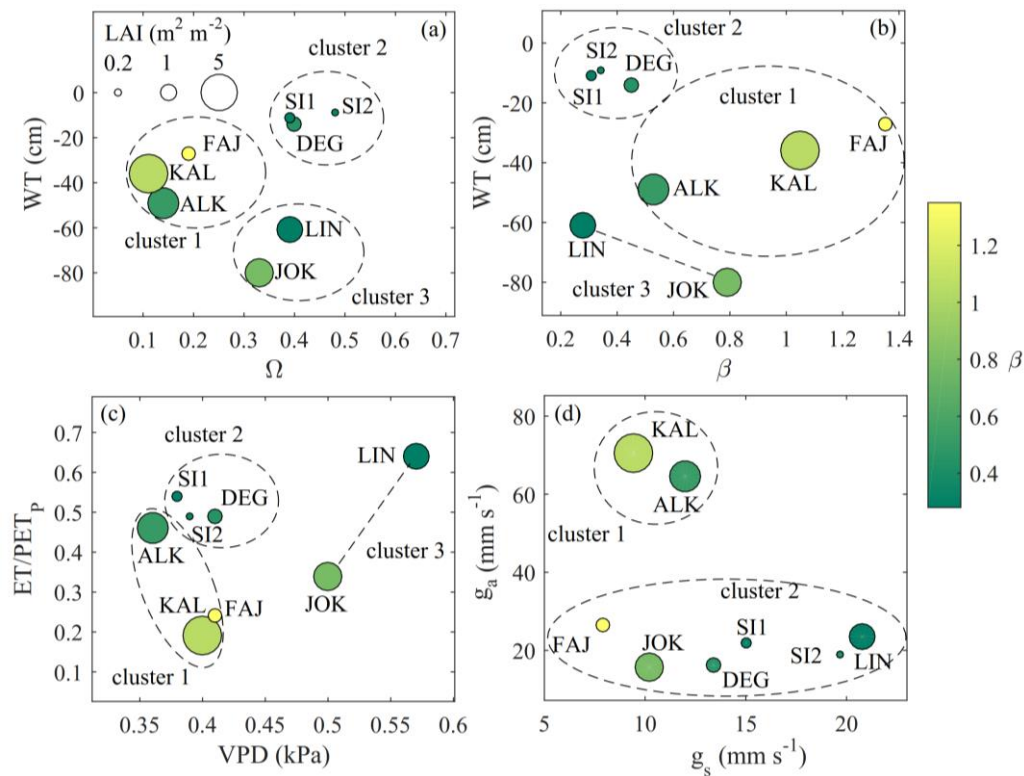


Figure 10. Meta-analysis of site-mean values for: (a) Jarvis-McNaughton decoupling parameter and water table position; (b) Bowen ratio and water table position; (c) actual to potential evapotranspiration *versus* vapour pressure deficit; (d) Bowen ratio and bulk surface conductance. Site marker sizes are proportional to leaf area index, while the colour indicates growing season cumulative Bowen ratio. The clusters were identified by eye.

rise coinciding with a small trough in g_s . At DEG, the year 2008 was dry from early spring, which is reflected in high May β and isolated weekly peaks in June and July.

Clustering of the peatland ecosystems based on mean parameter values

Mean growing season values of various ecophysiological factors are given in Table 4 and presented graphically in Figure 10. The first point of note is the emergence of three site clusters segregated by decoupling parameter and WT in Figure 10a: (i) ALK, KAL and FAJ; (ii) LIN and JOK; (iii) SI1, DEG and SI2. The first group includes the sites with moderate to significant tree biomass, intermediate WT , low decoupling parameter and high β . The second group has high graminoid biomass, the lowest water levels, intermediate Ω and low to intermediate β . The last group contains the wettest open mires with small biomass, high Ω and low β . The α_{PT} values relate inversely to β and thus give equivalent information. Similar clustering is seen in Figure 10b, where the dependency of β on WT is shown, although the site association in Clusters 1 and 3 is somewhat

lower than in Figure 10a. As before, the open mire cluster is very well defined.

In Figure 10c, the tendency for site separation is seen yet again in the relationship between ET/PET_p and VPD . JOK and LIN are farther apart than in the previous cases although, as in Figure 10a, b, the treeless and tree-covered clusters (1 and 2) are well defined. In general, evapotranspiration was closer to its potential value at sites experiencing higher vapour pressure deficit. While ET/PET_p means ranged from 0.25 to 0.62, ET/PET_{PM} was between 0.57 and 1.07.

Finally, Figure 10d shows the relationship between aerodynamic and surface conductances. The ecosystems differed widely in terms of vegetation canopy height and structure, which is reflected in the range of mean g_a values. It is interesting that, despite very different bulk surface conductances, LIN was much rougher than JOK by virtue of taller crop canopy, so that their mean Ω values were quite similar (0.39 and 0.33, respectively). With this presentation, the open mire/tree-covered clusters (1 and 2) remained, but the agricultural sites JOK and LIN now apparently transited to Cluster 2, which is indicated in the plot.

Table 4. Ecophysiological factors at the examined sites, given as means for the growing season. The annual minimum and maximum growing season values are shown in parentheses.

Site	β	VPD (kPa)	ET (mm day ⁻¹)	ET/PET_{PM}	ET/PET_P	α_{PT}	Ω	g_s (mm s ⁻¹)	g_a (mm s ⁻¹)	EF
ALK	0.53 (0.50–0.61)	0.36 (0.32–0.42)	2.4 (1.2–3.2)	1.07 (1.01–1.09)	0.47 (0.32–0.60)	0.98 (0.94–1.01)	0.14 (0.14–0.15)	12.0 (10.9–13.5)	64.5 (55.2–67.2)	0.51 (0.40–0.54)
KAL	1.05 (0.80–1.26)	0.40 (0.20–0.68)	1.6 (1.1–2.1)	1.00 (0.97–1.03)	0.21 (0.13–0.24)	0.74 (0.50–0.80)	0.11 (0.06–0.13)	9.4 (4.2–11.4)	70.4 (65.8–75.9)	0.36 (0.31–0.43)
JOK	0.79 (0.41–1.76)	0.50 (0.41–0.58)	1.3 (0.7–1.6)	0.57 (0.57–0.58)	0.34 (0.21–0.40)	0.88 (0.65–0.96)	0.33 (0.2–0.36)	10.2 (4.5–13.8)	15.8 (14.6–17.3)	0.34 (0.21–0.41)
LIN	0.28 (0.11–0.35)	0.57 (0.43–0.75)	2.8 (2.4–3.1)	0.72 (0.71–0.74)	0.62 (0.50–0.81)	1.20 (1.16–1.27)	0.39 (0.32–0.47)	20.8 (13.7–34.6)	23.4 (22–25.2)	0.51 (0.49–0.56)
DEG	0.45 (0.29–0.59)	0.41 (0.29–0.58)	1.7 (1.0–2.2)	0.88 (0.82–1.05)	0.53 (0.37–0.66)	1.01 (0.84–1.16)	0.40 (0.27–0.49)	13.4 (5.7–20.7)	16.3 (15.5–17.3)	0.48 (0.42–0.58)
SI1	0.31 (0.26–0.36)	0.38 (0.31–0.52)	1.7 (1.4–2.4)	0.76 (0.69–0.83)	0.57 (0.51–0.62)	1.15 (1.09–1.21)	0.39 (0.33–0.48)	15.0 (12.2–19.5)	21.9 (16.7–24.6)	0.48 (0.45–0.51)
SI2	0.34 (0.34–0.35)	0.39 (0.34–0.49)	1.8 (1.7–2.2)	0.63 (0.61–0.65)	0.54 (0.53–0.54)	1.12 (1.11–1.13)	0.48 (0.43–0.52)	19.7 (15.9–22.3)	19.0 (17.7–20.8)	0.46 (0.44–0.50)
FAJ	1.35 (1.17–1.51)	0.41 (0.33–0.59)	1.2 (1.2–1.3)	0.71 (0.69–0.73)	0.25 (0.25–0.26)	0.67 (0.66–0.71)	0.19 (0.17–0.21)	7.9 (7.1–8.5)	26.6 (24.5–28.7)	0.28 (0.26–0.30)

DISCUSSION

Management and natural development are the two main factors that determine the current ecological status of the eight examined peatlands. The characteristics of vegetation, hydrology and soil are reflected in energy partitioning, seasonality of energy fluxes, variability in evapotranspiration and sensitivity of the derived parameters (Ω , ET/PET_P or ET/PET_{PM} , g_s , EF , β , α_{PT}) to environmental forcing. As expected, several ecosystem groups can be distinguished based on their energy balance features: pristine open mires (SI1, DEG and SI2), tree-covered peatlands (ALK, KAL and FAJ), and agricultural peatlands (JOK and LIN). Generally, pristine open mire conditions favoured low β and high g_s . The mean Bowen ratio of the agricultural peatlands was also low, but associated with a smaller surface conductance. These sites displayed a strong seasonal variation in energy balance governed by crop phenology. Finally, the tree-covered peatlands showed the lowest surface conductance and the highest proportion of available energy converted into sensible heat flux.

Pristine open mires: SI1, DEG and SI2

The open pristine mires SI1, SI2 and DEG are tightly clustered with regard to each factor (Figure 10). Therefore, they set a “baseline” energy balance, against which the other sites can be compared, being characterised by high mean water level, continuous and well-humidified moss layer and an almost complete absence of tree cover, which explains the low Bowen ratio and bulk surface conductance. SI2, while formally classified as a bog, possessed the same features as, and resembled, the two fen sites.

Comparable values have been reported at other boreal sites. The 13.4–19.7 mm s⁻¹ range of g_s in the open pristine mires DEG, SI1 and SI2 is slightly lower than in a Danish riparian wetland (32 mm s⁻¹, Andersen *et al.* (2005)) and a Russian boreal bog (18.6–28.0 mm s⁻¹; Runkle *et al.* (2014)). The open mires were relatively poorly coupled to the atmosphere, having Ω about 0.4–0.5; again, somewhat lower than the values of 0.65–0.73 obtained by Runkle *et al.* (2014) at a site similar to SI2. Higher coupling has sometimes been observed in pristine mires: Kurbatova *et al.* (2002) observed an Ω of 0.4 at two oligotrophic bogs, and Brümmer *et al.* (2012) estimated $\Omega \approx 0.29$ –0.34 at the Mer Bleu bog.

A special feature of pristine mires is that moss surfaces may experience high water stress due to the intolerance of *Sphagnum* to even partial desiccation (Gerdol *et al.* 1996), which causes an increase in total

resistance to water vapour transport (*e.g.* Kettridge & Waddington 2014). However, in pristine mires, moisture usually remains in sufficient supply at the surface until the water table falls below a certain critical depth (Humphreys *et al.* 2006). Therefore, the smooth reduction of Ω after rain at DEG, SI1 and SI2 is probably due to a fast(er) vascular plant stress reaction rather than to slow desiccation of moss. Moreover, given the evidence of rapid *WT* drawdown after rain (Figure 8), the absence of a rapid seasonal change in *LE* at DEG, SI1 and SI2 (Figure 5c) indicates substantial resilience to drought.

Homeostatic behaviour of the wet open mires is also seen at seasonal scale as the stability of the Bowen ratio (Figure 5a); the May–September mean monthly β values are close to 0.4–0.6, with a slight upward trend towards autumn correlated with water table change. Similarly, stable β dynamics were reported for a Southern Finnish fen (Wu *et al.* 2010) and a central Siberian bog (Kurbatova *et al.* 2002), although a much more pronounced increase in β late in the growing season was observed at Mer Bleu bog (Admiral *et al.* 2006) and a bog in north-west Russia (Runkle *et al.* 2014).

However, the natural tolerances to moisture shortage can be overcome when the water table is too low, which is manifest as a step change in evapotranspiration. For example, during one drought event in 2006, the decoupling coefficient at DEG plunged steeply, reflecting a significant increase in surface resistance as *WT* fell below -25 cm during a prolonged rainless period (Figures 7b, 9a–c). In another dry year, the tolerance of SI1 was exceeded for a much shorter period of about one week, although *WT* was quite far below the summer average - perhaps because precipitation, while scarce, was frequent enough to prevent strong water stress. The value of *VPD* associated with this response was about 0.8 kPa at DEG and SI1, which is a fairly high value for these ecosystems. It was shown that the water table may draw down to the ‘critical’ depth where moisture is no longer transported efficiently from the saturated zone to the surface. In this situation rapid drying of the peat surface may ensue, eventually enabling the formation of a crust that does not conduct water, as described for a blanket bog by Sottocornola & Kiely (2010) and observed by the present authors at SI2. Such crusting might serve as another example of high sensitivity to summertime drawdown of the water table.

We also note that high water levels coincide with lower ecosystem–atmosphere coupling, as observed in the data from DEG, FAJ, SI1 and SI2 (Figure 7d). This could be simply attributed to sedge phenology - the water table is lowest around mid-summer, when

the sedge leaf area is at its maximum, providing the lowest r_a . Another explanation might be a reduction in surface roughness when the water table is high due to the appearance and/or increase in area of open water pools.

Tree-covered peatlands: ALK, KAL and FAJ

The three peatlands with tree cover illustrate the transition in the energy balance that has occurred on about half of the Fennoscandian peatland area - both naturally (fen to bog evolution) and through management (drainage, sometimes followed by afforestation). The raised bog FAJ is evolving towards the state of KAL, except that its low water table is a natural feature. Dominant features at ALK and KAL are 12–15 m tall pine stands developed after a 20–40 cm lowering of the water table *via* drainage created conditions suitable for trees. When the forest canopy is sufficiently large (in terms of leaf area index or biomass), it understandably dominates the ecosystem-scale biotic control on surface moisture exchange. Besides, the forest canopy shelters the ground, thereby impeding turbulent transport to some degree and enhancing storage change fluxes in comparison with open sites.

Boreal conifer tree stands use water conservatively. The forested peatlands ALK and KAL display similar values, having a comparatively low surface conductance of 10.1–13.4 mm s⁻¹, a Bowen ratio of 0.61–1.15 and a Priestley-Taylor α of 1.07–0.77. Equivalent values were found in a Finnish boreal Scots pine forest growing on mineral soil (Launiainen 2010). FAJ, a treed bog, resembles the managed forested sites. The relatively high coupling at FAJ ($\Omega = 0.19$) approaches that at KAL and ALK (0.11 and 0.14, respectively). A value observed by Brümmer *et al.* (2012) in a tree-covered fen ($\Omega = 0.16$, on average) falls near these estimates. The bulk surface conductance of only 7.9 mm s⁻¹ at FAJ is within the 4–14 mm s⁻¹ range observed at the Salmisuo fen (Wu *et al.* 2010). However, lower bulk surface conductance values elsewhere include 6.25 mm s⁻¹ reported for the Stormossen bog (Kellner 2001), and even 2.81–4.32 in a Canadian tree-covered fen and the Mer Bleu bog (Brümmer *et al.* 2012). Generally, the three sites ALK, KAL and FAJ had the most constrained evapotranspiration in this study. Out of all the sites, the smallest evaporative fraction (28 %) was found at FAJ, whereas at other sites it reached 35–50 % (Table 4).

The response of vegetation to water table position and precipitation is more important for evapotranspiration dynamics in the tree-covered peatlands than in the open peatlands. On a short timescale of ~10 days the dominating factor is the

physiological reaction of trees to increasing vapour pressure deficit, because the corresponding water level drawdown is not yet large enough to cause water stress for the trees (Launiainen 2010). Besides, when poor capillary water supply is combined with intense water loss at the surface, the topsoil may dry up within 2–3 days, again invoking the decoupling situation where *WT* no longer controls the moisture exchange at the surface (*e.g.* Price *et al.* 2003). The nonlinearity of these responses to *WT* is striking, as the rate of *WT* change is contrastingly constant after rain (Figure 8). Evidence of water supply breakdown is provided by the data for FAJ and KAL, where coupling with the atmosphere increases steeply with water table lowering until it reaches saturation at *WT* < -25 cm (Figure 7b), which is supported by the increase in α_{PT} (Figure 7a). In the FAJ case study (Figure 9g–i), such decoupling seemed to persist for most of the growing season, as β seemed to correlate with the precipitation pattern rather than with *WT*. Kettridge & Waddington (2014) observed sustained surface peat water content at *WT* values from 0 to -10 cm, but a step change upon further lowering. Qualitatively, the same process might be found in all peat soils, albeit with varying *WT* threshold and the frequency of decoupling cases probably depending on peat structure and mean *WT*. Besides, the tree cover at FAJ might be sparse enough to reduce overall *ET* instead of increasing it, by causing additional water level drawdown (Fay & Lavoie 2009, Limpens *et al.* 2014).

The Bowen ratio in tree-covered peatlands generally exceeded 0.5. However, the mean β value differed between sites, and it was 0.5 units lower at ALK than at KAL (Table 4). While the overstorey LAI and biomass were nearly equal, tree density was lower in ALK, meaning that the canopy there is more open. Given the higher forest floor LAI at ALK (2.0 *versus* 0.7 at KAL), this probably reflects more intense evapotranspiration from the forest floor. β showed a strong seasonal cycle (Figure 5a), as in the Stormossen bog, where it decreased gradually after an early summer peak (Kellner 2001). Such seasonality may be driven by a similar trend in tree canopy stomatal conductance, as it may increase in spring to resist the stress of low temperature combined with high *VPD* and photosynthetically active radiation (*PAR*). The typical summertime *WT* course is another likely reason.

Peat croplands: JOK and LIN

The two sites JOK and LIN, which have acquired their ecophysiological features in the course of agricultural exploitation, illustrate the influence of a graminoid vegetation cover. This mode of land use

implies a low water level (20–40 cm lower than in the forested sites) and the presence of a homogeneous crop canopy with drastic variation of LAI due to rapid growth and harvesting cycles. Such common features allow segregation of JOK and LIN based on their mean WT and Ω values, and the seasonal trend of β (Figures 4 and 9).

However, the similarity between JOK and LIN is limited due to their very different crop biomass and phenological development; besides, LIN was the only site in this study where the top peat layer was harvested. Reed canary grass (at LIN) has a higher biomass and water demand than the crops grown at JOK, and grows rapidly (typically up to 1.7 m tall). Biomass and leaf area differences between JOK and LIN explain the difference in evaporative fraction (0.34 and 0.51 on average, respectively). Disparity is also found in g_s (10.2 and 20.8 mm s⁻¹), α_{PT} (0.88 and 1.20) and, ultimately, in β (0.79 and 0.28). However, as the surface of LIN is aerodynamically rougher than that of JOK due to taller crops, their mean atmospheric coupling levels are quite similar (0.39 and 0.33, respectively). Nevertheless, the mean values indicate higher evapotranspiration constraints and thus lower LE at JOK than at LIN. See Figure 10 for a graphical representation of these differences between the two agricultural sites.

The topsoil at LIN may be permanently decoupled from the saturated zone (Gong *et al.* 2013). In our case, this implies a lack of direct linkage between the level of the water table and the water content of the surface peat layers because the saturated zone is too deep for continuous upward moisture transport to occur. Thus, topsoil wetness at LIN and JOK probably depends on the amount and timing of precipitation alone, which would explain the absence of identifiable trends related to water level.

The agricultural fields acquire dense vegetation cover that helps reduce the Bowen ratio to rather low levels between June and August, when crop biomass is at its peak before harvesting (Figure 5a). The growth of barley/forage grass at JOK is so intense that LAI reaches 5–6 m² m⁻² in July (Lohila *et al.* 2004). In this case, the high LAI creates conditions for complete domination of the energy balance by LE and, correspondingly, very low H and the lowest monthly β . This plunge in β is followed by a steep increase after the crops are harvested (typically in August–September, occasionally in June). Interannual variations in β are observed at JOK and predictably correlate with sowing and harvesting times, which vary from year to year (not shown). At LIN, in contrast, β is maintained at ~0.25 until later in the season as canary reed grass is not harvested until the spring of the following year. In fact, this

argument may be generalised: the clustering of seasonal curves (Figure 5c) is clearer for LE than for H because LE largely scales with LAI, which has a clear seasonality, so H may be seen as a mere residual of the energy balance.

Thus, the croplands show how the presence of a crop canopy can completely override the natural peatland energy exchange features, introducing seasonality and energy partitioning that are fully controlled by crop phenology. However, the specifics of behaviour appear to depend on crop type.

Implications of peatland management for climate: the energy balance aspect

From the above, the general finding is that the open mire energy balance features are, on the one hand, closely clustered, and on the other hand display relatively consistent seasonal patterns. The observation of divergent energy balances of the managed peatlands, together with their enhanced seasonality, has implications for local and regional climate.

Although the link between energy balance change and surface wetness remains poorly understood (*e.g.* Nijp *et al.* 2015), this study found indications that it depends on peatland type, with closer linkage in managed sites. High sensitivity to changes in WT and the effects of topsoil drying were observed at all sites except those with low mean WT (ALK, JOK). The deeper the post-management water level, the more the water table becomes dissociated from surface processes (Figures 7 and 8), as previously indicated by Gong *et al.* (2013).

In general, Ω values close to 0.4 at JOK, LIN, DEG, S11 and S12 indicate intermediate levels of ecosystem–atmosphere coupling, whereas the domination of low WT and stomatal control at ALK, KAL and FAJ supports a higher degree of coupling. In this context, the predictions of increasing future precipitation in northern Europe (Ruosteenoja *et al.* 2005) might lead to closer coupling between soil and atmosphere and thus partly compensate for the greater aridity of the drained sites.

Whilst being within the range of values obtained by Wilson *et al.* (2002a), β increased along the continuum: (a) pristine open mires (DEG, S11 and S12) – (b) peat croplands (JOK and LIN) – (c) tree-covered peatlands (ALK, KAL and FAJ). High β implies higher sensible heat flux, which promotes deepening of the boundary layer, and *vice versa*. Some earlier studies (*e.g.* Beringer *et al.* 2005) show that higher Bowen ratios may result from lower WT , as at the drained sites KAL and ALK (*via* drainage) and the treed bog FAJ (naturally). At peak LAI, the low Bowen ratio of the agricultural peatlands JOK

and LIN promotes a cooler and thinner atmospheric boundary layer and thus possibly offsets the warming effect of the carbon balance–climate feedback in agricultural peatlands to some extent. Ultimately, Ω and β are directly controlled by *WT* and the phenology of the dominant vegetation, which are both drastically altered after management activities.

CONCLUSIONS

The variety of management/land use strategies practiced on boreal peatlands has greatly diversified the previously more homogeneous pristine peatlands. Vegetation cover, soil and hydrology were all affected. This study used an array of sites, representative of the complex peatland mosaic found in the boreal region of Finland and Sweden, featuring pristine mires and drained forestry/agricultural peatlands. While sharing common origins as pristine mires, five of the ecosystems we examined have been driven by anthropic interference or natural evolution to evolve into distinctively different states.

Three distinct classes can be identified on the basis of features of the energy balance, namely: (a) open pristine mire, (b) tree-covered peatland and (c) agricultural peatland. The groups were defined by the responses of sensible and latent heat fluxes to environmental drivers and their seasonality. Pristine bogs were not differentiable as a separate class from fens, whereas the differences between the agricultural peatlands emphasised the relevance of crop type.

This method of classifying peatland together with a knowledge of management status can be used to predict the energy balance features of a site, given that post-management changes in the energy balance depend strongly on the land-use mode. The wide inter-ecosystem range in the parameters traditionally associated with climate (*e.g.* Bowen ratio, Jarvis-McNaughton decoupling parameter) implies that the strength and character of ecosystem–climate feedbacks might be as varied. The higher Bowen ratio of the tree-covered peatlands occasionally reduces water availability and potentially leads to regional warming. The strength of the climatic effects of agricultural peatland depends on crop type.

In efforts to conserve pristine peatlands and restore disturbed ones, the energy balance changes should be taken into account (Ramsar Convention Secretariat 2013, IPCC 2014). Therefore, any information about energy balance and climate feedbacks which improves predictions of the consequences of peatland management is currently in high demand amongst different research

communities. The results of the current study are relevant for practical applications including, but not limited to, surface–atmosphere exchange and climate models. However, we encourage the research community to make further assessments of the boreal peatland energy balance using larger datasets with wider geographical coverage.

ACKNOWLEDGEMENTS

The authors gratefully acknowledge: the Academy of Finland Centre of Excellence (Projects 272041 and 118780) and Academy Professor Projects (Numbers 1284701 and 1282842), ICOS-Finland (Project 281255) and CARB-ARC (Project 286190), Nordic Centre of Excellence DEFROST, the Faculty of Science and Forestry of the University of Eastern Finland, the Norwegian University of Technology (NTNU), the Centre for Studies of Carbon Cycle and Climate Interactions (LUCCI) financed by a Linnaeus grant (Swedish Research Council), and the CAPTURE project (296887, Carbon dynamics across Arctic landscape gradients: past, present and future). The studies at Degerö were financed by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Grant Number 2007-666), the Kempe Foundation and the Swedish University of Agricultural Sciences through the Long Term Environmental Monitoring Programme. The measurement data used in this study are available on request, from the authors.

REFERENCES

- Acreman, M.C., Harding, R.J., Lloyd, C.R. & McNeil, D.D. (2003) Evaporation characteristics of wetlands: experience from a wet grassland and a reedbed using eddy correlation measurements. *Hydrology and Earth System Sciences*, 7, 11–21.
- Admiral, S.W., Lafleur, P.M. & Roulet, N.T. (2006) Controls on latent heat flux and energy partitioning at a peat bog in eastern Canada. *Agricultural and Forest Meteorology*, 140, 308–321.
- Ahti T., Hämet-Ahti, L. & Jalas, J. (1968) Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici*, 5, 169–211.
- Alekseychik, P.K., Korrensalo, A., Mammarella, I., Vesala, T. & Tuittila, E.-S. (2017) Relationship between aerodynamic roughness length and bulk sedge leaf area index in a mixed-species boreal mire complex. *Geophysical Research Letters*, 44, 5836–5843.

- Alexandersson, H., Karlström, C. & Larsson-McCann, S. (1991) *Temperaturen och Nederbörden i Sverige 1961–90 Referensnormaler (Temperature and Precipitation Reference Norms in Sweden 1961–90)*. Meteorologi 81, Swedish Meteorological and Hydrological Institute (SMHI), Norrköping, 87 pp. (in Swedish).
- Andersen, H.E., Hansen, S. & Jensen, H.E. (2005) Evapotranspiration from a riparian fen wetland. *Nordic Hydrology*, 36, 121–135.
- Aubinet, M., Vesala, T. & Papale, D. (eds.) (2012) *Eddy Covariance: A Practical Guide to Measurement and Data Analysis*. Springer Netherlands, 438 pp.
- Aurela, M., Riutta, T., Laurila, T., Tuovinen, J.-P., Vesala, T., Tuittila, E.-S., Rinne, J., Haapanala, S. & Laine, J. (2007) CO₂ exchange of a sedge fen in southern Finland—the impact of a drought period. *Tellus B*, 59, 826–837.
- Bay, R.R. (1968) The hydrology of several peat deposits in northern Minnesota, U.S.A. In: *Proceedings of the Third International Peat Congress, Quebec, Canada*, Department of Energy, Mines and Resources, Ottawa, and National Research Council of Canada for International Peat Society, 212–218.
- Beleya, L.R. & Baird, A.J. (2006) Beyond “the limits to peat bog growth”: cross-scale feedback in peatland development. *Ecological Monographs*, 76, 299–322.
- Beringer, J., Chapin, F.S. III, Thompson, C.C. & McGuire, D.A. (2005) Surface energy exchanges along a tundra-forest transition and feedbacks to climate. *Agricultural and Forest Meteorology*, 131, 143–161.
- Betts, A.K., Desjardins, R.L. & Worth, D. (2007) Impact of agriculture, forest and cloud feedback on the surface energy budget in BOREAS. *Agricultural and Forest Meteorology*, 142, 156–169.
- Bleuten, W., Borren, W., Glaser, P.H., Tsuchihara, T., Lapshina, E.D., Mäkilä, M., Siegel, D., Joosten, H. & Wassen, M.J. (2006) Hydrological processes, nutrient flows and patterns of fens and bogs. In: Verhoeven, J.T.A., Beltman, B., Bobbink, R. & Whigham, D.F. (eds.) *Wetlands and Natural Resource Management*, Ecological Studies 190, Springer-Verlag Berlin Heidelberg, 183–204.
- Bonan, G.B., Oleson, K.W., Vertenstein, M., Levis, S., Zeng, X., Dai, Y., Dickinson, R.E. & Yang, Z.-L. (2002) The land surface climatology of the Community Land Model coupled to the NCAR Community Climate Model. *Journal of Climate*, 15, 3123–3149.
- Bridgman, S.D., Pastor, J., Updegraff, K., Malterer, T.J., Johnson, K., Harth, C. & Chen, J. (1999) Ecosystem control over temperature and energy flux in northern peatlands. *Ecological Applications*, 9, 1345–1358.
- Brümmer, C., Black, T.A., Jassal, R.S., Grant, N.J., Spittlehouse, D.L., Chen, B., Nestic, Z., Amiro, B.D., Arain, M.A., Barr, A.G., Bourque, C.P.-A., Coursolle, C., Dunn, A.L., Flanagan, L.B., Humphreys, E.R., Lafleur, P.M., Margolis, H.A., McCaughey, J.H. & Wofsy, S.C. (2012) How climate and vegetation type influence evapotranspiration and water use efficiency in Canadian forest, peatland and grassland ecosystems. *Agricultural and Forest Meteorology*, 153, 14–30.
- Burba, G.G., Verma, S.B. & Kim, J. (1999) A comparative study of surface energy fluxes of three communities (*Phragmites australis*, *Scirpus acutus*, and open water) in a prairie wetland ecosystem. *Wetlands*, 19, 451–457.
- Chapin, F.S. III, McGuire, A.D., Randerson, J., Pielke, R.Sr., Baldocchi, D., Hobbie, S.E., Roulet, N., Eugster, W., Kasischke, E., Rastetter, E.B., Zimov, S.A. & Running, S.W. (2000) Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology*, 6(S1), 211–223.
- Desjardins, R.L., Sivakumar, M.V.K. & de Kimpe, C. (2007) The contribution of agriculture to the state of climate: Workshop summary and recommendations. *Agricultural and Forest Meteorology*, 142, 314–324.
- Drebs, A., Nordlund, A., Karlsson, P., Helminen, J. & Rissanen, P. (2002) Climatic statistics of Finland. In: *Tilastoja Suomen ilmastosta 1971–2000 (Climatological Statistics of Finland 1971–2000)*, Finnish Meteorological Institute, Helsinki, 99 pp.
- Eugster, W., Rouse W.R., Pielke, R.A.Sr., McFadden, J.P., Baldocchi, D.D., Kittel, T.G.F., Chapin, F.S. III, Liston, G.E., Vidale, P.L., Vaganov, E. & Chambers, S. (2000) Land-atmosphere energy exchange in Arctic tundra and boreal forest: available data and feedbacks to climate. *Global Change Biology*, 6(S1), 84–115.
- Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Gross, P., Grünwald, T., Hollinger, D., Jensen, N.-O., Katul, G., Keronen, P., Kowalski, A., Lai, C.T., Law, B.E., Meyers, T., Moncrieff, J., Moors, E., Munger, J.T., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Tenhunen, J., Tu, K., Verma, S., Vesala, T., Wilson, K. & Wofsy, S.

- (2001) Gap filling strategies for long term energy flux data sets. *Agricultural and Forest Meteorology*, 107, 71–77.
- Fay, E. & Lavoie, C. (2009) The impact of birch seedlings on evapotranspiration from a mined peatland: an experimental study in southern Quebec, Canada. *Mires and Peat*, 5(03), 1–7.
- Foken, T. (2008) The energy balance closure problem: An overview. *Ecological Applications*, 18, 1351–1367.
- Garratt, J.R. & Hicks, B.B. (1973) Momentum, heat and water transfer to and from natural and artificial surfaces. *Quarterly Journal of the Royal Meteorological Society*, 99, 680–687.
- Gerdol, R., Bonor, A., Gualandri, R. & Pancaldi, S. (1996) CO₂ exchange, photosynthetic pigment composition, and cell ultrastructure of *Sphagnum* mosses during dehydration and subsequent rehydration. *Canadian Journal of Botany*, 74, 726–734.
- Gong, J., Shurpali, N.J., Kellomäki, S., Wang, K., Zhang, C., Abdus Salam, M.M. & Martikainen, P.J. (2013) High sensitivity of peat moisture content to seasonal climate in a cutaway peatland cultivated with a perennial crop (*Phalaris arundinaceae*, L.): A modeling study. *Agricultural and Forest Meteorology*, 180, 225–235.
- Granberg, G., Grip, H., Ottosson Lofvenius, M., Sundh, I., Svensson, B.H. & Nilsson, M. (1999) A simple model for simulation of water content, soil frost, and soil temperatures in boreal mixed mires. *Water Resources Research*, 35, 3771–3782.
- Harazono, Y., Yoshimoto, M., Mano, M., Vourlitis, G.L. & Oechel, W.C. (1998) Characteristics of energy and water budgets over wet sedge and tussock tundra ecosystems at North Slope in Alaska. *Hydrological Processes*, 12, 2163–2183.
- Hari, P. & Kulmala, M. (2005) Station for measuring ecosystem–atmosphere relations (SMEAR II). *Boreal Environment Research*, 10, 315–322.
- Haslwanter, A., Hammerle, A. & Wohlfahrt, G. (2009) Open-path vs. closed-path eddy covariance measurements of the net ecosystem carbon dioxide and water vapour exchange: A long-term perspective. *Agricultural and Forest Meteorology*, 149, 291–302.
- Haverd, V., Cuntz, M., Leuning, R. & Keith, H. (2007) Air and biomass heat storage fluxes in a forest canopy: Calculation within a soil vegetation atmosphere transfer model. *Agricultural and Forest Meteorology*, 147, 125–139.
- Hayward, P.M. & Clymo, R.S. (1982) Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology. *Proceedings of the Royal Society of London B*, 215, 299–325.
- Humphreys, E.R., Lafleur, P.M., Flanagan, L.B., Hedstrom, N., Syed, K.H., Glenn, A.J. & Granger, R. (2006) Summer carbon dioxide and water vapor fluxes across a range of northern peatlands. *Journal of Geophysical Research*, 111, G04011, 1–16, doi: 10.1029/2005JG000111.
- IPCC (2014) *2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories: Wetlands*. Hiraiishi, T., Krug, T., Tanabe, K., Srivastava, N., Baasansuren, J., Fukuda, M. & Troxler, T.G. (eds.), IPCC, Switzerland. Online at: <https://www.ipcc-nggip.iges.or.jp/public/wetlands/>, accessed 25 July 2018.
- Järveoja, J., Peichl, M., Maddison, M., Teemusk, A. & Mander, Ü. (2016) Full carbon and greenhouse gas balances of fertilized and nonfertilized reed canary grass cultivations on an abandoned peat extraction area in a dry year. *Global Change Biology Bioenergy*, 8, 952–968, doi: 10.1111/gcbb.12308.
- Jarvis, P.G. & McNaughton, K.G. (1986) Stomatal control of transpiration: Scaling up from leaf to region. *Advances in Ecological Research*, 15, 1–49.
- Kasurinen, V., Alfredsen, K., Kolari, P., Mammarella, I., Alekseychik, P., Rinne, J., Vesala, T., Bernier, P., Boike, J., Langer, M., Marchesini, L.B., van Huissteden, K., Dolman, H., Sachs, T., Ohta, T., Varlagin, A., Rocha, A., Arain, A., Oechel, W., Lund, M., Grelle, A., Lindroth, A., Black, A., Aurela, M., Laurila, T., Lohila, A. & Berninger, F. (2014) Latent heat exchange in the boreal and arctic biomes. *Global Change Biology*, 20, 3439–3456, doi: 10.1111/gcb.12640.
- Kellner, E. (2001) *Surface Energy Exchange and Hydrology of a Poor Sphagnum Mire*. PhD thesis, Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology 657, Acta Universitatis Upsaliensis, Uppsala, 38 pp., ISBN 91-554-5121-7.
- Kettridge, N. & Waddington, J.M. (2014) Towards quantifying the negative feedback regulation of peatland evaporation to drought. *Hydrological Processes*, 28, 3728–3740.
- Korrensalo, A., Alekseychik, P., Hájek, T., Alekseychik, P., Rinne, J., Vesala, T., Mehtätalo, L., Mammarella, I. & Tuittila, E.-S. (2017) Species-specific temporal variation in photosynthesis as a moderator of peatland carbon sequestration. *Biogeosciences*, 14, 257–269.
- Kurbatova, J., Arneth, A., Vygodskaya, N.N., Kolle, O., Varlagin, A.V., Milyukova, I.M., Tchebakova,

- N.M., Schulze, E.-D. & Lloyd, J. (2002) Comparative ecosystem–atmosphere exchange of energy and mass in a European Russian and a central Siberian bog I. Interseasonal and interannual variability of energy and latent heat fluxes during the snowfree period. *Tellus B*, 54, 497–513.
- Lafleur, P.M. (2008) Connecting atmosphere and wetland: Energy and water vapour exchange. *Geography Compass*, 2, 1027–1057, doi: 10.1111/j.1749-8198.2007.00132.x.
- Lafleur, P.M., Hember, R.A., Admiral, S.W. & Roulet, N.T. (2005) Annual and seasonal variability in evapotranspiration and water table at a shrub-covered bog in southern Ontario, Canada. *Hydrological Processes*, 19, 3533–3550.
- Laine, A.M., Bubier, J., Riutta, T., Nilsson, M.B., Moore, T.R., Vasander, H. and Tuittila, E.-S. (2012) Abundance and composition of plant biomass as potential controls for mire net ecosystem CO₂ exchange. *Botany*, 90, 63–74, doi: 10.1139/b11-068.
- Lange, O.L., Lösch, R., Schulze, E.-D. & Kappen, L. (1971) Responses of stomata to changes in humidity. *Planta*, 100, 76–86.
- Launiainen, S. (2010) Seasonal and inter-annual variability of energy exchange above a boreal Scots pine forest. *Biogeosciences*, 7, 3921–3940.
- Launiainen, S., Katul, G.G., Kolari, P., Lindroth, A., Lohila, A., Aurela, M., Varlagin, A., Grelle, A. & Vesala, T. (2016) Do the energy fluxes and surface conductance of boreal coniferous forests in Europe scale with leaf area? *Global Change Biology*, 22, 4096–4113.
- Liljedahl, A.K., Hinzman, L.D., Harazono, Y., Zona, D., Tweedie, C.E., Hollister, R.D., Engstrom, R. and Oechel, W.C. (2011) Nonlinear controls on evapotranspiration in arctic coastal wetlands. *Biogeosciences*, 8, 3375–3389.
- Limpens, J., Holmgren, M., Jacobs, C.M.J., Van der Zee, S.E.A.T.M., Karofeld, E. & Berendse, F. (2014) How does tree density affect water loss of peatlands? A mesocosm experiment. *PLoS ONE*, 9(3), e91748, 1–11, doi: 10.1371/journal.pone.0091748.
- Lindroth, A., Mölder, M. & Lagergren, F. (2010) Heat storage in forest biomass improves energy balance closure. *Biogeosciences*, 7, 301–313.
- Lohila, A., Aurela, M., Tuovinen, J.-P. & Laurila, T. (2004) Annual CO₂ exchange of a peat field growing spring barley or perennial forage grass. *Journal of Geophysical Research*, 109, D18116, 1–13, doi: 10.1029/2004jd004715.
- Lohila, A., Aurela, M., Regina, K., Tuovinen, J.-P. & Laurila, T. (2007) Wintertime CO₂ exchange in a boreal agricultural peat soil. *Tellus B*, 59, 860–873.
- Lohila, A., Minkkinen, K., Aurela, M., Tuovinen, J.-P., Penttilä, T., Ojanen, P. & Laurila, T. (2011) Greenhouse gas flux measurements in a forestry-drained peatland indicate a large carbon sink. *Biogeosciences*, 8, 3203–3218.
- Lund, M., Lindroth, A., Christensen, T.R. & Ström, L. (2007) Annual CO₂ balance of a temperate bog. *Tellus B*, 59, 804–811.
- Lund, M., Christensen, T.R., Mastepanov, M., Lindroth, A. & Ström, L. (2009) Effects of N and P fertilization on the greenhouse gas exchange in two northern peatlands with contrasting N deposition rates. *Biogeosciences*, 6, 2135–2144.
- Maljanen, M., Sigurdsson, B.D., Guðmundsson, J., Óskarsson, H., Huttunen, J.T. & Martikainen, P.J. (2010) Greenhouse gas balances of managed peatlands in the Nordic countries - present knowledge and gaps. *Biogeosciences*, 7, 2711–2738.
- Minkkinen, K., Byrne, K.A. & Trettin, C.C. (2008) Climate impacts of peatland forestry. In: Strack, M. (ed.) *Peatlands and Climate Change*, International Peat Society, Jyväskylä, 98–122.
- Mölder, M. & Kellner, E. (2002) Excess resistance of bog surfaces in central Sweden. *Agricultural and Forest Meteorology*, 112, 23–30.
- Monteith, J. (1965) Evaporation and environment. *Symposia of the Society for Experimental Biology*, 19, 205–234.
- Nijp, J.J., Limpens, J., Metselaar, K., Peichl, M., Nilsson, M.B., van der Zee, S.E.A.T.M. & Berendse, F. (2015) Rain events decrease boreal peatland net CO₂ uptake through reduced light availability. *Global Change Biology*, 21, 2309–2320, doi: 10.1111/gcb.12864.
- Ochsener, T.E., Sauer, T.J. & Horton, R. (2007) Soil heat storage measurements in energy balance studies. *Agronomy Journal*, 99, 311–319.
- Ojanen, P., Minkkinen, K., Lohila, A., Badorek, T. & Penttilä, T. (2012) Chamber measured soil respiration: A useful tool for estimating the carbon balance of peatland forest soils? *Forest Ecology and Management*, 277, 132–140.
- Ojanen, P., Minkkinen, K. & Penttilä, T. (2013) The current greenhouse gas impact of forestry-drained boreal peatlands. *Forest Ecology and Management*, 289, 201–208.
- Oren, R., Sperry, J.S., Katul, G.G., Pataki, D.E., Ewers, B.E., Phillips, N. & Schäfer, K.V.R. (1999) Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell & Environment*, 22, 1515–1526.
- Owen, P.R. & Thomson, W.R. (1963) Heat transfer

- across rough surfaces. *Journal of Fluid Mechanics*, 15, 321–334.
- Peichl, M., Sagerfors, J., Lindroth, A., Buffam, I., Grelle, A., Klemedtsson, L., Laudon, H. & Nilsson, M.B. (2013) Energy exchange and water budget partitioning in a boreal minerogenic mire. *Journal of Geophysical Research: Biogeosciences*, 118, 1–13, doi: 10.1029/2012JG002073.
- Peichl, M., Öquist, M., Ottosson Löfvenius, M., Ilstedt, U., Sagerfors, J., Grelle, A., Lindroth, A. & Nilsson, M.B. (2014) A 12-year record reveals pre-growing season temperature and water table level threshold effects on the net carbon dioxide uptake in a boreal fen. *Environmental Research Letters*, 9(5), 055006, 1–11, doi: 10.1088/1748-9326/1089/1085/055006.
- Peichl, M., Sonnentag, O. & Nilsson, M.B. (2015) Bringing color into the picture: Using digital repeat photography to investigate phenology controls of the carbon dioxide exchange in a boreal mire. *Ecosystems*, 18 115–131.
- Penman, H.L. (1948) Natural evaporation from open water, bare soil and grass. *Proceedings of the Royal Society of London A*, 193, 120–145, doi: 10.1098/rspa.1948.0037.
- Pereira, A.R. (2004) The Priestley-Taylor parameter and the decoupling factor for estimating reference evapotranspiration. *Agricultural and Forest Meteorology*, 125, 305–313.
- 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., Marcolla, B., Friborg, T., Rinne, J., Hatala Matthes, J., Merbold, L., Meijide, A., Kiely, G., Sottocornola, M., Sachs, T., Zona, D., Varlagin, A., Lai, D.Y.F., Veenendaal, E., Parmentier, F.-J.W., Skiba, U., Lund, M., Hensen, A., van Huissteden, J., Flanagan, L.B., Shurpali, N.J., Grünwald, T., Humphreys, E.R., Jackowicz-Korczyński, M., Aurela, M.A., Laurila, T., Grüning, C., Corradi, C.A.R., Schrier-Uijl, A.P., Christensen, T.R., Tamstorf, M.P., Mastepanov, M., Martikainen, P.J., Verma, S.B., Bernhofer, C. & Cescatti, A. (2015) The uncertain climate footprint of wetlands under human pressure. *PNAS: Proceedings of the National Academy of Sciences of the United States of America*, 112(15), 4594–4599, doi: 10.1073/pnas.1416267112.
- Price, J.S. (1991) Evaporation from a blanket bog in a foggy coastal environment. *Boundary-Layer Meteorology*, 57, 391–406.
- Price, J.S., Heathwaite, A.L. & Baird, A.J. (2003) Hydrological processes in abandoned and restored peatlands: An overview of management approaches. *Wetlands Ecology and Management*, 11, 65–83.
- Priestley, C.H.B. & Taylor, R.J. (1972) On the assessment of surface heat flux and evaporation using large-scale parameters. *Monthly Weather Review*, 100, 81–92.
- Raddatz, R.L., Papakyriakou, T.N., Swystun, K.A. & Tenuta, M. (2009) Evapotranspiration from a wetland tundra sedge fen: Surface resistance of peat for land-surface schemes. *Agricultural and Forest Meteorology*, 149, 851–861.
- Ramsar Convention Secretariat (2013) *The Ramsar Convention Manual: a Guide to the Convention on Wetlands (Ramsar, Iran, 1971)*, 6th edition. Ramsar Convention Secretariat, Gland, Switzerland, 109 pp.
- Rinne, J., Riutta, T., Pihlatie, M., Aurela, M., Haapanala, S., Tuovinen, J.-P., Tuittila, E.-S. & Vesala, T. (2007) Annual cycle of methane emission from a boreal fen measured by the eddy covariance technique. *Tellus B*, 59, 449–457.
- Riutta, T., Laine, J., Aurela, M., Rinne, J., Vesala, T., Laurila, T., Haapanala, S., Pihlatie, M. & Tuittila, E.-S. (2007) Spatial variation in plant community functions regulates carbon gas dynamics in a boreal fen ecosystem. *Tellus B*, 59, 838–852.
- Runkle, B.R.K., Wille, C., Gažovič, M., Wilmking, M. & Kutzbach, L. (2014) The surface energy balance and its drivers in a boreal peatland fen of northwestern Russia. *Journal of Hydrology*, 511, 359–373.
- Ruosteenoja, K., Jylhä, K. & Tuomenvirta, H. (2005) *Climate Scenarios for FINADAPT Studies of Climate Change Adaptation. FINADAPT Working Paper 15*. Finnish Environment Institute Mimeographs 345, 38 pp. ISBN: 952-11-2127-0, ISSN: 1455-0792.
- Sagerfors, J., Lindroth, A., Grelle, A., Klemedtsson, L., Weslien, P. & Nilsson, M. (2008) Annual CO₂ exchange between a nutrient-poor, minerotrophic, boreal mire and the atmosphere. *Journal of Geophysical Research*, 113, G01001, 1–15, doi: 10.1029/2006JG000306.
- Seppä, H. (2002) Mires of Finland: Regional and local controls of vegetation, landforms, and long-term dynamics. *Fennia - International Journal of Geography*, 180(1–2), 43–60. Online at: <https://fennia.journal.fi/article/view/3763>
- Shimoyama, K., Hiyama, T., Fukushima, Y. & Inoue, G. (2003) Seasonal and interannual variation in water vapor and heat fluxes in a West Siberian continental bog. *Journal of Geophysical Research*, 108(D20), 4648, 1–13, doi: 10.1029/2003JD003485.
- Shurpali, N.J., Hyvonen, N.P., Huttunen, J.T., Clement, R.J., Reichstein, M., Nykänen, H., Biasi,

- C. & Martikainen, P.J. (2009) Cultivation of a perennial grass for bioenergy on a boreal organic soil - carbon sink or source? *Global Change Biology Bioenergy*, 1, 35–50, doi: 10.1111/j.1757-1707.2009.01003.x.
- Shurpali, N.J., Biasi, C., Jokinen, S., Hyvönen, N. & Martikainen, P.J. (2013) Linking water vapor and CO₂ exchange from a perennial bioenergy crop on a drained organic soil in eastern Finland. *Agricultural and Forest Meteorology*, 168, 47–58.
- Sottocornola, M. & Kiely, G. (2010) Energy fluxes and evaporation mechanisms in an Atlantic blanket bog in southwestern Ireland. *Water Resources Research*, 46, W11524, 1–13, doi: 10.1029/2010WR009078.
- Thom, A.S. (1975) Momentum, mass and heat exchange of plant communities. In: Monteith J. (ed.) *Vegetation and the Atmosphere, Volume 1*, Academic Press, London, 57–109.
- Verma, S.B. (1989) Aerodynamic resistances to transfers of heat, mass and momentum. In: Black, T.A., Spittlehouse, D.L., Novak, M.D. & Price, D.T. (eds.) *Estimation of Areal Evaporation, Proceedings of a Workshop held at Vancouver, August 1987*, Publication No. 177, International Association of Hydrological Sciences (IAHS), Wallingford, 13–20.
- Waddington, J.M., Morris, P.J., Kettridge, N., Granath, G., Thompson, D.K. & Moore, P.A. (2015) Hydrological feedbacks in northern peatlands. *Ecohydrology*, 8, 113–127.
- Weiss, R., Alm, J., Laiho, R. & Laine, J. (1998) Modeling moisture retention in peat soils. *Soil Science Society of America Journal*, 62, 305–313.
- Wilson, K.B., Baldocchi, D.B., Aubinet, M., Berbigier, P., Bernhofer, C., Dolman, H., Falge, E., Field, C., Goldstein, A., Granier, A., Grelle, A., Halldor, T., Hollinger, D., Katul, G., Law, B.E., Lindroth, A., Meyers, T., Moncrieff, J., Monson, R., Oechel, W., Tenhunen, J., Valentini, R., Verma, S., Vesala, T. & Wofsy, S. (2002a) Energy partitioning between latent and sensible heat flux during the warm season at FLUXNET sites. *Water Resources Research*, 38(12), 1294, 30.1–30.11, doi: 10.1029/2001WR000989.
- Wilson, K., Goldstein, A., Falge, E., Aubinet, M., Baldocchi, D., Berbigier, P., Bernhofer, C., Ceulemans, R., Dolman, H., Field, C., Grelle, A., Ibrom, A., Law, B.E., Kowalski, A., Meyers, T., Moncrieff, J., Monson, R., Oechel, W., Tenhunen, J., Valentini, R. & Verma, S. (2002b) Energy balance closure at FLUXNET sites. *Agricultural and Forest Meteorology*, 113, 223–243.
- Wu, J., Kutzbach, L., Jager, D., Wille, C. & Wilmking, M. (2010) Evapotranspiration dynamics in a boreal peatland and its impact on the water and energy balance. *Journal of Geophysical Research*, 115, G04038, 1–18, doi: 10.1029/2009JG001075.
- Yurova, A., Wolf, A., Sagerfors, J. & Nilsson, M. (2007) Variations in net ecosystem exchange of carbon dioxide in a boreal mire: Modeling mechanisms linked to water table position. *Journal of Geophysical Research*, 112, G02025, 1–13, doi:10.1029/2006JG000342.

Submitted 29 Jan 2018, final revision 10 Jun 2018
 Editor: Jonathan Price

Author for correspondence: Dr Pavel Alekseychik, Institute for Atmospheric and Earth System Research (INAR) / Physics, Faculty of Science, P.O. Box 68, FI-00014 University of Helsinki, Finland.
 Tel: +358406520950; E-mail: pavel.alekseychik@helsinki.fi