



Title	Effects of the expansion of vascular plants in Sphagnum-dominated bog on evapotranspiration
Author(s)	Hirano, Takashi; Yamada, Hiroyuki; Takada, Masayuki; Fujimura, Yoshiyasu; Fujita, Hiroko; Takahashi, Hidenori
Citation	Agricultural and forest meteorology, 220, 90-100 https://doi.org/10.1016/j.agrformet.2016.01.039
Issue Date	2016-04-15
Doc URL	http://hdl.handle.net/2115/68178
Rights	© 2016, Elsevier. This manuscript version is made available under the CC-BY-NC-ND 4.0 license http://creativecommons.org/licenses/by-nc-nd/4.0/
Rights(URL)	http://creativecommons.org/licenses/by-nc-nd/4.0/
Type	article (author version)
File Information	AFM220_90-100.pdf



[Instructions for use](#)

1 **Effects of the expansion of vascular plants in *Sphagnum*-dominated bog on**
2 **evapotranspiration**

3

4 Takashi Hirano¹, Hiroyuki Yamada¹, Masayuki Takada², Yoshiyasu Fujimura³, Hiroko Fujita⁴
5 and Hidenori Takahashi⁵

6

7 ¹Research Faculty of Agriculture, Hokkaido University, Sapporo, Japan

8 ²Faculty of Humanity and Environment, Hosei University, Tokyo, Japan

9 ³R & D Center, Nippon Koei, Ibaraki, Japan

10 ⁴Field Science Center for Northern Biosphere, Hokkaido University, Sapporo, Japan

11 ⁵Hokkaido Institute of Hydro-Climate, Sapporo, Japan

12

13 Corresponding to: T. Hirano, Research Faculty of Agriculture, Hokkaido University, Sapporo

14 060-8589, Japan. (hirano@env.agr.hokudai.ac.jp)

15

16 **Abstract**

17

18 Plant succession triggered by drainage, which results in the expansion or invasion of vascular
19 plants, has been reported from many peatlands. However, the effects of the vascular plant's
20 expansion on evapotranspiration (ET), which is a key component of the water balance of
21 ombrotrophic bog, is still contradictory. To investigate the effects, ET was measured at a
22 *Sphagnum*-dominated bog and an adjacent transition peatland dominated by *Sasa*, dwarf
23 bamboo, in Hokkaido Island, northern Japan, using the eddy covariance technique during the
24 four growing seasons from 2007 through 2010. Cumulative gap-filled ET during a snow-free
25 period of 6.5 months was 362 (2008) and 374 mm (2010) at the *Sphagnum* site and 300 (2008)
26 and 372 mm (2010) at the *Sasa* site. In the mid-growing season (late June to mid-September)
27 with the highest leaf area index (LAI) at the *Sasa* site, ET was 2.14 ± 0.03 (mean \pm 1 standard
28 deviation of the four years) and 1.92 ± 0.19 mm d⁻¹, respectively, at the *Sphagnum* and *Sasa*
29 sites. ET was smaller at the *Sasa* site, except for 2010 with an unusual hot wet summer; mean
30 air temperature and precipitation were higher than their 30-year normal values by 1.75°C and
31 172 mm, respectively. At the *Sphagnum* site, ET was stable despite such interannual variation
32 in meteorological conditions. However, ET increased significantly at the *Sasa* site in 2010
33 probably because of LAI increase due to the enhanced growth of *Sasa* plants. The ET increase
34 at the *Sasa* site suggests that ET will increase at the *Sasa*-dominated area, if the future warming
35 environment accompanies more precipitation.

36

37 **Keywords**

38 Dwarf bamboo, eddy covariance, energy balance, groundwater level, peatland, warming

39

40 **1. Introduction**

41 Peatlands are distributed worldwide with the total area of 4.16×10^6 km², of which more than
42 80% are localized in the temperate to subarctic regions of the Northern Hemisphere (Ryden and
43 Jeglum, 2006). Northern peatland has accumulated soil organic carbon as peat under cool and
44 waterlogged conditions over millennia, mainly during Holocene, up to 455-500 Pg (Gorham,
45 1991; Yu, 2012), which is equivalent to about 30% of global soil organic carbon (1550 Pg) (Lal,
46 2004). Therefore, a slight change of the huge carbon pool due to environmental perturbations
47 can lead to a considerable change in the global carbon balance (Dorrepaal et al., 2009; Frohling
48 et al., 2006; Heikkinen et al., 2004). As a result, northern peatland has attracted attentions from
49 the viewpoint of global warming concerns during the last few decades (Charman et al., 2013;
50 Frohling et al., 2011; Limpens et al., 2008; Mitsch et al., 2012).

51 The carbon balance of peatlands is strongly affected by local hydrology (Bozkurt et al.,
52 2001; Fenner and Freeman, 2011; Limpens et al., 2008). Groundwater level (GWL), which
53 usually remains high in natural peatlands, controls the thickness of an unsaturated peat layer
54 with groundwater. Thus, lowering of GWL potentially enhances oxidative peat decomposition
55 and, consequently increases carbon dioxide (CO₂) emissions to the atmosphere. Land-use
56 change of natural peatlands for agriculture and forestry accompanies GWL lowering through
57 drainage. In addition, lowered GWL tends to change the composition and productivity of plant
58 communities; biomass of mesic vascular plants increases, leading to a decline of *Sphagnum*
59 species chiefly by shading (Laine et al., 1995; Murphy et al., 2009; Talbot et al., 2010). Change
60 in plant communities, which accompanies an increase in vascular plants at the expense of
61 bryophytes and lichens, is also expected under warming climate (Berg et al., 2009; Walker et
62 al., 2006; Ward et al., 2013). The increase of vascular plants will change the carbon and water
63 balances of peatlands (Ward et al., 2013).

64 In peatlands, evapotranspiration (ET) is a key component of the water balance and much

65 contributes to GWL variation, especially in ombrotrophic bogs (Lafleur, 2008). Comparative
66 studies on ET from two adjacent bogs dominated by *Sphagnum* moss and covered or mixed
67 with vascular plants, respectively, showed inconsistent results. Takagi et al. (1999), who applied
68 the Bowen ratio / energy balance method, reported that a bog covered by invading dwarf
69 bamboo (*Sasa palmata*) increased ET in comparison with a native open bog in northern Japan,
70 which was attributed to larger leaf area index (LAI) of dwarf bamboo. In contrast, Strilesky and
71 Humphreys (2012), who applied the eddy covariance method, reported that ET was smaller in
72 a treed bog with stunted black spruce as an overstory than in an open bog in southern Canada.
73 The different results probably arose from different biotic and abiotic conditions, including plant
74 species, LAI, climate, hydrology and measurement duration. If the invasion of mesic vascular
75 plants increases ET, bogs are forced to dry, and consequently the invasion would accelerate,
76 resulting in a positive feedback. Also, GWL tends to decrease as the density of vascular plants
77 increases because of increase in rainfall interception (Farrick and Price, 2009). Ongoing global
78 warming potentially increases ET as a result of increasing water vapor deficit (VPD) due to
79 temperature rise and shortened snow cover duration (Waddington et al., 2015), and also alters
80 plant communities in peatlands (Walker et al., 2006; Ward et al., 2013). Because ET strongly
81 affects the carbon pool of peatlands via GWL, it is crucial to understand the effects of the
82 vegetation alteration on ET. However, our knowledge on the effects is still insufficient owing
83 to a limited number of related field studies. Therefore, well-designed comparative experiments
84 at adjacent peatlands are essential (Moore et al., 2013).

85 We measured sensible (H) and latent heat (LE) fluxes using the eddy covariance technique
86 and determined ET and energy balance at two adjacent sites, where *Sphagnum* moss and mesic
87 dwarf bamboo (*Sasa*) dominate, respectively, in an ombrotrophic bog area (Takagi et al., 1999)
88 in Hokkaido, the northernmost island of Japan, during four growing seasons from 2007 through
89 2010, including a record-breaking hot summer in 2010 (Otomi et al., 2012). In the ombrotrophic

90 bog area, *Sasa* plants have been expanding since the 1960s, when a drainage channel was
91 excavated (Tsuji, 1963). *Sasa* expansion after drainage is common in many other bog areas in
92 Hokkaido Island (Fujita, 2006). Here, we show the results of the field experiment and discuss
93 the seasonal and interannual variations of ET in combination with phenology and climatic
94 variability, and environmental control on ET using bulk surface conductance. Finally, we assess
95 whether the invasion of *Sasa* plants into a *Sphagnum*-dominated bog increases ET and discuss
96 the impact on ET of the abnormally hot summer that is predicted in the near future under
97 ongoing global warming.

98

99 **2. Materials and methods**

100 **2.1. Study area**

101 The field experiment was conducted at a *Sphagnum*-dominated open bog and an adjacent *Sasa*-
102 dominated transition peatland (45°06'N, 141°42'E; 6-7 m alt.) in Sarobetsu Mire with the total
103 area of 6658 ha, in which bog with flat lawn is the dominant peatland type (Fujita et al., 2007),
104 in northern Hokkaido Island, northern Japan. The mire was bordered by drainage ditches, a
105 river and pastures. About 6-m-thick peat has accumulated for 4000-5000 years (Ohira, 1995;
106 Sakaguchi et al., 1985). *Sphagnum papillosum* Linbd., *S. magellanicum* Brid. and *Carex*
107 *middendorffi* were dominant in the *Sphagnum*-dominated bog (*Sphagnum* site), whereas *Sasa*
108 *palmata* densely covered *Sphagnum* species on the ground along with *Myrica gale* L. var.
109 *tomentosa* C.D.C and *Ilex crenata* Thunb. var. *radicans* (Nakai ex H. Hara) Murai as overstory
110 in the *Sasa*-dominated peatland (*Sasa* site) (Fujimura et al., 2012). The canopy heights ranged
111 from 0.2 (*Sphagnum*) to 0.45 m (*Sasa*) at the maximum. The ground surface was partly covered
112 with *Carex*'s leaf litter in spring at *Sphagnum* site, whereas the ground was densely mulched
113 with *Sasa*'s leaf litter throughout the growing season at *Sasa* site. *S. palmata* spreads rhizomes
114 for vegetative propagation. The rhizomes and roots of *Sasa* plants penetrated 0.3-0.4 m into

115 peat soil, yet they concentrated within the top 0.2 m (Takakuwa and Ito, 1986). *Sasa* plants
116 began to expand into the open bog area in the 1960s with the excavation of drainage ditches for
117 agriculture (Tsujii, 1963). The *Sasa*-dominated area has increased by 15.8% between 1977 and
118 2003 (Fujimura et al., 2013); the *Sasa* expansion was attributable to the alteration of
119 groundwater regime through drainage (Fujimura et al., 2012; Takada et al., 2012).

120 Annual mean air temperature and annual precipitation are 6.1°C and 1073 mm (1981-2010)
121 at Toyotomi meteorological observatory, which is located about 6 km east of the study sites.
122 The minimum and maximum mean monthly temperatures are -6.5 (January and February) and
123 19.6°C (August), respectively. Precipitation in the growing season from May through October
124 accounts for 57% of annual precipitation. Annual maximum snow depth reaches about 1 m. The
125 deep snow accumulation inhibits the development of *Sphagnum* hummocks (Yabe and Uemura,
126 2001; Yazaki and Yabe, 2012).

127

128 **2.2. Field measurement**

129 A small mast was built for the following measurement at *Sphagnum* site and the adjacent *Sasa*
130 site, respectively; the location of *Sphagnum* site is the same as site B in the work by Takagi et
131 al. (1999). The two eddy covariance towers were located about 600 m apart. Fetch for flux
132 measurement was more than 200 m in all directions for both masts.

133 Eddy fluxes of sensible heat (H) and latent heat (LE) were measured on the masts of
134 *Sphagnum* and *Sasa* sites, respectively, during the four snow-free periods from late June to early
135 November in 2007, late April to mid-November in 2008, mid-April to early November in 2009
136 and late April to early November in 2010. Data were missing after October in 2007 at *Sphagnum*
137 site and after mid-September in 2009 at *Sasa* site owing to system malfunction. A sonic
138 anemometer-thermometer (CSAT3; Campbell Scientific Inc., Logan, UT, USA) and an open-
139 path CO₂ / H₂O analyzer (LI7500; LICOR Inc., Lincoln, NE, USA) were used to measure H

140 and LE. Sensor signals were recorded using a datalogger (CR1000; Campbell Scientific Inc.)
141 at 10 Hz. The open-path analyzer was calibrated every year using a dew-point generator (LI810;
142 LICOR Inc.) in a laboratory.

143 Global solar radiation (R_g) and net radiation (R_n) were measured with a radiometer (CNR-
144 1; Kipp & Zonen, Delft, the Netherlands) at a height of 1.8 m. Air temperature and relative
145 humidity were measured with a platinum resistance thermometer and a capacitive hygrometer
146 (HMP45; Vaisala, Helsinki, Finland) installed in a non-ventilated radiation shield (DTR503A;
147 Vaisala) at a height of 1.5 m. Precipitation was measured with a tipping-bucket rain gauge
148 (TE525; Campbell Scientific Inc.) at a height of 1.5 m only at *Sasa* site. Wind velocity and
149 direction were measured with a cup anemometer and a wind vane (03002-47A; R. M. Young
150 Co., Traverse, MI, USA) at a height of 2.3 m only at *Sasa* site. Soil temperature was measured
151 with thermocouples at depths of 2, 5, 10 and 40 cm. Volumetric soil water content (SWC) was
152 measured with a TDR sensor (CS616; Campbell Scientific Inc.) buried at a depth of 5 cm and
153 calibrated using the oven-drying method. Heat flux was measured with a heat flow transducer
154 (HFT1.1; REBS, Bellevue, WS, USA) at a depth of 10 cm. Sensor signals were measured every
155 10 s, and their means were recorded every 10 min using a datalogger (CR10X; Campbell
156 Scientific Inc.). Groundwater level (GWL), which was determined as a distance between the
157 ground (reference) and groundwater surfaces, was measured every 10 or 30 min with a pressure
158 sensor (HTV-020KP; SENSEZ Co., Tokyo, Japan) and a datalogger (VR-71; T&D Corporation,
159 Matsumoto, Japan). The belowground sensors were installed within 5 m from each mast.
160 Measurements other than eddy flux were conducted continuously from late June 2007.

161 Leaf area index (LAI) was measured monthly from April through November in 2009 and
162 2010 at *Sasa* site. At 70 points within 20 m from the mast, LAI was measured with a plant
163 canopy analyzer (LAI2000; LICOR Inc.) with five replications. LAI of vascular plants above
164 *Sphagnum* moss was also measured several times at *Sphagnum* site in 2009 and 2010.

165

166 **2.3. Flux calculation**

167 Half-hourly mean H and LE were calculated according to the following procedures: 1) removal
168 of noise spikes (Vickers and Mahrt, 1997), 2) planar fit rotation (Wilczak et al., 2001), 3) water
169 vapor correction for H (Hignett, 1992), 4) correction for high- and low-frequency losses using
170 a theoretical transfer function (Massman, 2000), 5) covariance calculation using a block average
171 and 6) density fluctuation correction for LE (Webb et al., 1980). The sensitivity of an open-path
172 analyzer (LI7500) for water vapor density was calibrated by comparing half-hourly mean water
173 vapor densities from the LI7500 and a slow-response thermometer / hygrometer (HMP45)
174 (Hirano et al., 2015; Iwata et al., 2012); the latter sensor was expected to be more accurate on
175 a half-hourly basis. Data were only compared under the neutral condition of atmospheric
176 stability, because the LI7500 was installed 0.5-0.8 m higher than the HMP45.

177 Soil heat flux at the ground surface (G ; W m^{-2}) was calculated as the sum of heat flux at a
178 depth of 10 cm (G_{10} ; W m^{-2}) and heat storage change of the topmost soil layer of 10-cm
179 thickness using the following equations.

$$180 \quad G = G_{10} + C \cdot z \cdot \frac{dT}{dt} \quad (1)$$

$$181 \quad C = C_s \cdot x_s + C_w \cdot x_w + C_g \cdot (1 - x_s - x_w) \quad (2)$$

182 where C is heat capacity of the soil layer ($\text{J m}^{-3} \text{K}^{-1}$), z is the thickness of the soil layer (= 0.1
183 m), dT is temporal change in a mean of soil temperatures (K) at depths of 2, 5 and 10 cm at a
184 time interval of dt (= 1800 s), C_s , C_w and C_g are heat capacities of solid (= 2.5×10^6), liquid (=
185 4.2×10^6) and gas (= 1.2×10^3) ($\text{J m}^{-3} \text{K}^{-1}$) (de Vries, 1963), respectively, and x_s and x_w are
186 volumetric fractions of solid and liquid ($\text{m}^3 \text{m}^{-3}$), respectively. x_w corresponds to SWC, and x_s
187 was determined to be 0.038 and 0.075, respectively, for *Sphagnum* and *Sasa* sites, from soil-
188 core sampling. The bulk densities of the topmost soil layer of 10-cm thickness were 53.6
189 (*Sphagnum*) and 113.2 kg m^{-3} (*Sasa*).

190

191 **2.4. Quality control and gap filling of flux data**

192 We first excluded flux data measured in the rain. Next, we calculated the difference between
193 covariances determined from the whole interval of 30 min and six intervals of 5 min. Flux data
194 were excluded, if covariance difference was larger than 250% (Foken and Wichura, 1996).
195 Consequently, the survival rates of flux data in the daytime ($R_g \geq 5 \text{ W m}^{-2}$) and nighttime ($R_g <$
196 5 W m^{-2}) were $81 \pm 11\%$ (mean ± 1 standard deviation (SD) of the four growing seasons) and
197 $66 \pm 11\%$, respectively, for H , and $78 \pm 10\%$ and $46 \pm 7\%$, respectively, for LE at *Sphagnum*
198 site. At *Sasa* site, the rates were $81 \pm 10\%$ (daytime) and $76 \pm 5\%$ (nighttime) for H , and $79 \pm$
199 10% (daytime) and $60 \pm 2\%$ (nighttime) for LE. Data gaps of both H and LE were filled half-
200 hourly by the look-up table (LUT) method using R_n and water vapor pressure deficit (VPD) as
201 predictors (Falge et al., 2001). The R_n and VPD were grouped into ten and three classes,
202 respectively. The LUT was created everyday using a moving window of 15 days for each site.

203

204 **2.5. Energy imbalance**

205 Energy balance was not closed at both sites, as at many of other flux sites (Stoy et al., 2013;
206 Wilson et al., 2002). To confirm the degree of energy imbalance, eddy energy flux ($H + LE$)
207 was plotted against available energy ($R_n - G$) using half-hourly measured data in each year. As
208 a result, all linear correlations had r^2 values higher than 0.9; their slopes and intercepts were
209 0.73 ± 0.02 (mean ± 1 SD of the four years) and $5.5 \pm 2.5 \text{ W m}^{-2}$, respectively, at *Sphagnum*
210 site, and 0.74 ± 0.02 and $1.6 \pm 3.5 \text{ W m}^{-2}$, respectively, at *Sasa* site.

211

212 **2.6. Calculation of bulk surface conductance**

213 Bulk surface conductance (G_s) (Monteith, 1965) was calculated in no-rain conditions to
214 interpret the seasonal variation and environmental response of ET. G_s (m s^{-1}) stands for the

215 integration of each individual leaf's stomatal conductance for transpiration and surface wetness
 216 for evaporation, which was calculated backward from the Penman-Monteith (PM) equation
 217 (Eqn. 3) (Ryu et al., 2008).

$$218 \quad \frac{1}{G_s} = \frac{1}{G_a} \left[\frac{\varepsilon(R_n - G) + \rho C_p G_a \frac{VPD}{\gamma}}{LE} - \varepsilon - 1 \right] \quad (3)$$

219 where G_a is bulk aerodynamic conductance (m s^{-1}), ε is s / γ , s is the slope of relationship
 220 between saturation water vapor pressure and temperature (kPa K^{-1}), γ is psychrometric constant
 221 ($= 0.067 \text{ kPa K}^{-1}$), ρ is air density (kg m^{-3}), C_p is specific heat of air at constant pressure ($= 1007$
 222 $\text{J kg}^{-1} \text{K}^{-1}$), and VPD is vapor pressure deficit (kPa). G_a was calculated using the following
 223 equation (Humphreys *et al.*, 2006).

$$224 \quad G_a = \left[\frac{2}{\kappa u^*} \left(\frac{dh}{dv} \right)^{\frac{2}{3}} + \frac{u}{u^{*2}} \right]^{-1} \quad (4)$$

225 where κ is von Karman constant ($=0.4$), u^* is friction velocity (m s^{-1}), dh is thermal diffusivity,
 226 dv is molecular diffusivity of water vapor and u is mean wind velocity (m s^{-1}). The ratio of dh
 227 and dv (dh/dv) was set at 0.89 (Humphreys *et al.*, 2006). To separate dry G_s from all G_s data, G_s
 228 was excluded if there was antecedent precipitation within six hours. Potential ET (PET) was
 229 calculated by setting G_s infinite in the PM equation.

230

231 **3. Results**

232 **3.1 Environmental and vegetative conditions**

233 Anomalies of air temperature and precipitation from their 30-year normal values are shown in
 234 Table 1. During the growing season from May through October, the anomalies of air
 235 temperature and precipitation ranged from -0.37 (2009) to $+1.02^\circ\text{C}$ (2010) and -195 (2008) to
 236 $+152 \text{ mm}$ (2010), respectively. Summer (July-August) air temperature differed by 3.3°C
 237 between 2009 and 2010. Thus, climate of each year is summarized as a warm growing season
 238 in 2007, a dry summer and fall in 2008, a cool summer in 2009 and a hot wet summer in 2010.

239 Groundwater level (GWL) and volumetric soil water content (SWC) at a depth of 5 cm
240 fluctuated in accordance with precipitation events (Fig. 1). The maximum and minimum GWLs
241 recorded during the four snow-free periods were -0.31 (2008) and 0.05 m (2010), respectively,
242 at *Sphagnum* site, and -0.43 (2010) and -0.09 m (2010), respectively, at *Sasa* site (Figs. 1a-d).
243 On the whole, GWL was higher by 0.1-0.2 m at *Sphagnum* site. On the other hand, SWC was
244 much lower at *Sphagnum* site except when GWL rose above -0.05 m. The surface soil of
245 *Sphagnum* site mainly consisted of undecomposed *Sphagnum* remains and thus had low bulk
246 density (53.6 kg m^{-3}), which resulted in high hydraulic conductivity. Therefore, GWL's small
247 variations caused large fluctuations in SWC, if GWL was above -0.1 m.

248 Leaf area index (LAI) showed a clear seasonal variation with a peak in September at *Sasa*
249 site (Fig. 2); peak values were 4.3 and 4.6 $\text{m}^2 \text{ m}^{-2}$, respectively, in 2009 and 2010. The
250 seasonality was closely related to the phenology of dominant *Sasa* plants, whose height peaked
251 at 0.35 to 0.45 m, respectively, in 2009 and 2010. In May, LAI was significantly higher in 2009
252 probably because of higher temperature in May. However, leaf expansion rapidly progressed
253 during the summer of 2010 because of the very hot weather, which resulted in significant
254 differences in July and August between the two years. At *Sphagnum* site, LAI of vascular plants
255 in September was 1.2 and 1.4 $\text{m}^2 \text{ m}^{-2}$, respectively, in 2009 and 2010.

256

257 **3.2. Energy fluxes and evapotranspiration**

258 Daily evapotranspiration (ET) of the two sites showed similar seasonal variation, whereas ET
259 was smaller at *Sasa* site during the early growing season (Figs. 1i-l). Daily ET peaked at 4.14,
260 3.60, 3.79 and 3.83 mm d^{-1} , respectively, in 2007, 2008, 2009 and 2010 at *Sphagnum* site, which
261 occurred on between DOY 161 (2010) and 208 (2008). At *Sasa* site, respective peak ETs were
262 3.27, 2.86, 3.43 and 3.97 mm d^{-1} in the years, which occurred on between DOY 186 (2007) and
263 264 (2010). On average, peak ET was smaller by 0.46 mm d^{-1} and delayed for 47 days at *Sasa*

264 site.

265 Figure 3 shows ensemble-averaged diurnal variations in energy fluxes. All fluxes showed
266 significant differences around midday (1000-1400) among the three seasons at each site (Table
267 2). Net radiation (R_n) decreased from the early to late seasons via the mid-season (Figs. 3a-c)
268 in accordance with decreasing solar elevation. The diurnal range of soil heat flux (G) was larger
269 at *Sphagnum* site, whereas daily means were almost the same (Figs. 3d-f). Sensible heat flux
270 (H) decreased from the early to late seasons especially at *Sasa* site (Figs. 3g-i). In the early and
271 mid-seasons, H was larger at *Sasa* site than at *Sphagnum* site. In the late season, nighttime H
272 became more negative at both sites. Latent heat flux (LE) increased from the early to mid-
273 seasons and decreased toward the late season (Figs. 3j-l). These seasonal variations of H and
274 LE were more pronounced at *Sasa* site. Contrary to H , LE was smaller at *Sasa* site in the early
275 and mid-seasons; midday LE was smaller by about 50 W m^{-2} at *Sasa* site in the early season
276 (Table 2). Daily gap-filled ET was largest in the mid-season; it was smallest in the late and early
277 seasons, respectively, at *Sphagnum* and *Sasa* sites (Table 2). Similarly, the ratio of ET and
278 potential ET (ET / PET), which refers to a measure of the ability of the atmosphere to remove
279 water from the surface (Takami et al., 2013; Wu et al., 2010), showed different seasonality
280 between the sites. The highest ratio appeared in the mid-season at *Sphagnum* site, whereas it
281 was in the late season at *Sasa* site (Table 2).

282

283 **3.3. Interannual variation in evapotranspiration**

284 Cumulative ET for 201 days is shown in Table 3. Under a dry condition in 2008, ET accounted
285 for 82 and 68% of precipitation, respectively, at *Sphagnum* and *Sasa* sites. In contrast, under a
286 wet condition in 2010, ET accounted for only 46% at both sites. In 2009 with normal
287 precipitation, ET at *Sphagnum* site accounted for 62% of precipitation. Cumulative ET was 62
288 mm more at *Sphagnum* site than at *Sasa* site in 2008, whereas ETs of both sites were almost the

289 same in 2010. ET increased by 12 and 72 mm between 2008 and 2010, respectively, at
290 *Sphagnum* and *Sasa* sites. Low coefficient of variance (CV) (2.1%) of the cumulative ETs
291 (2008-2010) indicates that interannual variation in ET is small at *Sphagnum* site despite larger
292 interannual variation in precipitation (CV = 24.2%).

293 Energy fluxes are averaged for a common measurement period of 86 days from June 21
294 through September 14 in each year together with environmental factors (Table 4) to compare
295 them between sites and among years. In this peak growth period (Fig. 2), precipitation was
296 largest in 2010 and smallest in 2008. Air temperature showed significant interannual difference;
297 it was highest in 2010 and lowest in 2009. VPD around midday (1000-1400) was higher at *Sasa*
298 site. VPD increased in dry 2008 and decreased in wet 2010. SWC was higher at *Sasa* site. R_n
299 showed no significant difference between sites and among years. H was larger at *Sasa* site and
300 largest in dry 2008. LE and ET showed a significant interaction between inter-site and
301 interannual differences; it was larger at *Sphagnum* site except for 2010, a hot and wet year.
302 Bowen ratio ($\beta = H / LE$) was larger at *Sasa* site and largest in dry 2008 and smallest in wet
303 2010. Mean ETs during the four years were 2.14 ± 0.03 (mean ± 1 SD; CV = 1.5%) and $1.92 \pm$
304 0.19 mm d^{-1} (CV = 9.9%), respectively, at *Sphagnum* and *Sasa* sites. The CV was much lower
305 at *Sphagnum* site, which indicates that ET was stable at *Sphagnum* site despite large variation
306 in precipitation (CV = 35.5%).

307

308 **3.4. Nighttime evapotranspiration**

309 On average, LE was positive even during the nighttime and larger in the late growing season at
310 both sites (Figs. 3j-l). Monthly mean ETs in the nighttime ($R_g < 5 \text{ W m}^{-2}$) were stable at 0.0085-
311 0.0095 and 0.0071-0.0077 mm h^{-1} , respectively, at *Sphagnum* and *Sasa* sites from May through
312 July, whereas it increased up to 0.028 and 0.025 mm h^{-1} in October, respectively, at *Sphagnum*
313 and *Sasa* sites by a factor of three or more (Fig. 4a). Accordingly, the ratio of nighttime and

314 daytime ETs increased from 0.06-0.09 until August to 0.29 and 0.27 in October, respectively,
315 at *Sphagnum* and *Sasa* sites (Fig. 4b). The increase in the late season would be related to
316 increases in VPD and wind velocity in the nighttime (Fig. 4c), which was reflected on more
317 negative nighttime H in the late season (Fig. 3i). Throughout the growing season from May
318 through October, mean nighttime ETs were 0.015 ± 0.013 (mean \pm 1 SD) and 0.014 ± 0.013
319 mm h^{-1} , respectively, at *Sphagnum* and *Sasa* sites, which correspond to the nighttime / daytime
320 ratios of 0.10 and 0.11, respectively.

321

322 **3.5. Control on evapotranspiration**

323 ET or LE depended on available energy (E_a) at both sites. The r^2 values of simple regression
324 between LE and E_a using half-hourly data were 0.80 ± 0.02 (mean \pm 1 SD of the four growing
325 seasons) and 0.74 ± 0.06 , respectively, at *Sphagnum* and *Sasa* sites (data not shown). On
326 average, LE consumed 47.1 ± 0.7 and $41.7 \pm 4.7\%$ of E_a , respectively, at *Sphagnum* and *Sasa*
327 sites. LE normalized by E_a was insensitive to GWL or SWC at both sites ($r^2 < 0.05$, data not
328 shown).

329 Dry surface conductance (G_s) in the daytime was significantly higher at *Sphagnum* site
330 than at *Sasa* site, except for hot wet 2010 (Tables 2 and 4 and Fig. 5). In 2010, dry G_s values of
331 the two sites were almost the same in the mid- and late seasons (Figs. 5e-f) mainly because of
332 the large increase of G_s at the *Sasa* site, whereas the increase of G_s was limited at *Sphagnum*
333 site. Dry G_s tended to decrease in the afternoon only at *Sasa* site, except for the early season of
334 2010 (Fig. 5d). Figure 6 shows the relationships between daytime dry G_s and VPD in the mid-
335 season, in which data were divided into two groups by GWL. The shapes of the relationships
336 were different between sites, years or GWL groups. At *Sphagnum* site in 2007-2009, dry G_s
337 simply decreased with VPD independently of GWL (Fig. 5a). In 2010, when GWL was high
338 (Fig. 1d), dry G_s was higher in the higher GWL group (> -0.05 m) (Fig. 5b). Dry G_s was

339 relatively insensitive to VPD in comparison with that in 2007-2009. At *Sasa* site, in contrast,
340 dry G_s was almost stable when VPD was lower than about 7 hPa, then decreased with VPD in
341 2007-2009 (Fig. 5c). Dry G_s was much higher and more sensitive to VPD in 2010 than in 2007-
342 2009 (Fig. 5d); G_s was higher in the higher GWL group (> -0.28 m). To directly examine the
343 relationship between dry G_s and GWL, they were plotted within a limited VPD range. Although
344 the relationship was significant in 2007-2009 at both sites, the r^2 values were very low (< 0.02)
345 (data not shown). On the other hand, dry G_s was positively correlated with GWL in 2010,
346 though the r^2 values were still relatively low, especially at *Sasa* site (Fig. 7).

347

348 **4. Discussion**

349 **4.1. Comparison of ET with other studies**

350 Our study sites were located in the same bog area as Takagi et al. (1999) studied; they measured
351 LE at *Sphagnum*- and *Sasa*-dominated areas intermittently with the Bowen ratio / energy
352 balance method and predicted ET using daytime data for 152 days from June through October
353 in 1995. As a result, cumulative precipitation and ETs at the *Sphagnum* and *Sasa* areas were
354 reported to be 559, 285 and 372 mm, respectively. During the same period of 152 days, our
355 results show that cumulative ETs were 294 (2008), 299 (2009) and 297 (2010) mm at *Sphagnum*
356 site and 246 (2008) and 307 (2010) mm at *Sasa* sites. Cumulative precipitations in the three
357 years were 333, 530 and 702 mm, respectively. ETs from the two studies were almost the same
358 for the *Sphagnum* open bog. For the *Sasa* area, however, ET from Takagi et al. (1999) was 65
359 mm larger than our ET even in 2010, when precipitation was 143 mm more than that in 1995.
360 Even after energy imbalance correction according to Twine et al. (2000), ET in 2010 was still
361 smaller by 24 mm. The discrepancy in cumulative ET was chiefly attributable to methodology,
362 because LAI and GWL shown by Takagi et al. (1999) are similar with those of our result.

363 In comparison with ETs from peatlands located at similar latitudes, mean gap-filled ET

364 at *Sphagnum* site during the peak growth period from mid-June through mid-September (2.14
365 mm d⁻¹, Table 4) was smaller than summer ET of 2.5 mm d⁻¹ in a low-shrub bog with higher
366 LAI in Ontario (45°25'N) (Humphreys et al., 2006) and growing season ET of about 2.5 mm d⁻¹
367 (mean of 13 bog sites) (Lafleur, 2008). Maximum ETs of 3.60 to 4.14 mm d⁻¹ at *Sphagnum*
368 site (Fig. 1) were smaller than those in an open peatland in Michigan (4.8-5.0 mm d⁻¹, 46°12'N)
369 (Moore et al., 2013), a shrub-covered bog in Ontario (4-5 mm d⁻¹, 45°24'N) (Lafleur et al.,
370 2005) and an open fen in Minnesota (4.8 mm d⁻¹, 47°32'N) (Kim and Verma, 1996). The smaller
371 ET in this study is partly attributable to lower VPD due to coastal climate.

372

373 **4.2. Seasonal variations**

374 Energy balance varied through the growing season. H decreased from the early season toward
375 the late season, whereas LE peaked in the mid-season (Table 2 and Fig. 3). As a result, Bowen
376 ratio (β) decreased greatly between the early and mid-season; midday β decreased from 1.17 to
377 0.67 at *Sphagnum* site and from 1.92 to 0.89 at *Sasa* site (Table 2). Seasonal decrease in β from
378 May (0.9) to September (0.6) was also reported for a *Sphagnum* mire in Sweden (Kellner, 2001).
379 At *Sphagnum* site, no change occurred in dry G_s between the early and mid-seasons (Table 2),
380 whereas LAI of vascular plants probably increased (Takagi et al., 1999). Therefore, the change
381 in β at *Sphagnum* site was chiefly caused by the seasonality of atmospheric conditions.
382 Saturation water vapor pressure increases exponentially with air temperature, thus the ratio of
383 vapor pressure difference and temperature difference between the surface and a height tends to
384 increase as air temperature rises, which results in lower β (Kondo, 1976; Shimoyama, 2003).
385 The partition of E_a into H and LE depends on bulk aerodynamic conductance (G_a). E_a is
386 partitioned more into H when G_a is high, because H is directly governed by G_a , whereas LE is
387 governed by G_a in combination with G_s . Accordingly, lower G_a due to lower wind velocity (data
388 not shown) decreased β in the mid-season. At *Sasa* site, β decreased more than at *Sphagnum*

389 site between the early and mid-seasons. In addition to the change in meteorological conditions,
390 the seasonal variation of G_s due to LAI increase also contributed to the β variation at *Sasa* site
391 (Table 2 and Fig. 2).

392

393 **4.3. Nighttime evapotranspiration**

394 Nighttime ET sharply increased in the late growing season at both sites (Fig. 4a). As a result,
395 the ratio of ET between the nighttime and daytime increased up to 27-29% in October (Fig. 4b).
396 The seasonal variation was chiefly caused by increases in VPD and wind velocity (Fig. 4c)
397 (Kobayashi et al., 2007; Novick et al., 2009). In addition, the wetter surface in the late season,
398 which can be inferred from more precipitation (Table 1), likely contributed to the increase of
399 nighttime ET. The nighttime / daytime ratio averaged out at 10-11% during the whole growing
400 season, which was larger than the annual ratios of 8-9% in three adjacent ecosystems consisting
401 of conifer and hardwood forests and a grassland (Novick et al., 2009). Although uncertainties
402 due to gap filling is large in nighttime ET (Novick et al., 2009), nighttime ETs after gap filling
403 by the look-up table method accounted for 8.5 and 7.8% of daily total ET, respectively, at
404 *Sphagnum* and *Sasa* sites on average throughout the growing season. This fact implies that ET
405 or energy fluxes should be measured carefully even in the nighttime in this study area,
406 especially in the late season.

407

408 **4.4. Control on evapotranspiration**

409 On a half-hourly basis, E_a accounted for 80% and 74% of temporal variations in LE,
410 respectively, at *Sphagnum* and *Sasa* sites. Such dependence of LE on R_n or E_a was reported for
411 many wetlands (e.g. Mackay et al., 2007; Zhou et al., 2010; Humphreys et al., 2006; Kurbatova
412 et al., 2002). LE normalized by E_a (LE / E_a) was insensitive to GWL, as Takagi et al. (1999)
413 measured at the same site. Similar insensitivity of ET to GWL was reported for other

414 *Sphagnum*-dominated peatlands (e.g. Wu et al., 2010; Brown et al., 2010; Moore et al., 2013)
415 and can be explained by efficient capillary water rise within *Sphagnum* moss (Price and
416 Whittington, 2010; Yazaki et al., 2006). Figure 6a, however, suggests that the wicking water
417 cannot compensate evaporation under high VPD conditions, leading to low G_s because of the
418 resultant dryness of the moss surface to some extent. On the other hand, under high GWL
419 conditions in 2010 (> -0.13 m, Fig. 1d), the sensitivity of dry G_s to VPD reduced (Fig. 6b),
420 because the limitation of capillary uptake was relaxed (Liljedal et al., 2011).

421 As for *Sasa* site, dry G_s remained almost constant until VPD increased up to 7-8 hPa in
422 2007-2009 (Fig. 6c), which suggests that stomatal conductance of *Sasa* plants was insensitive
423 to VPD within this low VPD range. In 2010, although the relationship was unclear ($r^2 = 0.07$,
424 Fig. 7b), dry G_s was higher under higher GWL conditions (from -0.28 to -0.09 m) than lower
425 conditions (-0.35 to -0.28 m) (Fig. 6d). Because the root systems of *Sasa* plants concentrated in
426 the top 0.2 m of soil (Takakuwa and Ito, 1986), the rhizosphere was unsaturated by about 50%
427 even at the maximum GWL of -0.09 m. Thus, the higher GWL possibly caused *Sasa* plants to
428 absorb soil water more easily despite some anaerobic stress and resulted in higher G_s . However,
429 the higher G_s would be more sensitive to VPD, because higher G_s potentially accompanies more
430 water loss by enhanced transpiration and can cause partial stomatal closure. As a result, dry G_s
431 decreased linearly with VPD under higher GWL conditions in 2010 (Fig. 6d). It was reported
432 that ET and G_s decreased with GWL, if GWL lowered beyond a threshold, such as -0.65 m for
433 ET (Lafleur et al., 2005; Humphreys et al., 2006) and -0.4 to -0.5 m for G_s (Waddington et al.,
434 2015), respectively. However, such a threshold was not found in this study, because GWL
435 remained relatively high above -0.3 and -0.45 m, respectively, at *Sphagnum* and *Sasa* sites (Fig.
436 1).

437

438 **4.5. Effects of *Sasa* invasion**

439 ET had been measured simultaneously at the two adjacent sites with different dominant species
440 to investigate the effects of the invasion of *Sasa* plants into a *Sphagnum*-dominated bog.
441 Because the two sites were only 600 m apart each other, they can be considered to have been
442 subjected to the same synoptic weather conditions. Cumulative ET for about 6.5 months of the
443 snow-free period was larger at *Sphagnum* site (362 mm) than at *Sasa* site (300 mm) in 2008
444 with a dry summer and fall, whereas they were almost the same (374 vs. 372 mm) in 2010 with
445 an abnormally hot wet summer (Table 3). During the peak growth period, ET was also larger at
446 *Sphagnum* site in 2007, 2008 and 2009, except for in 2010 (Table 4). These results indicate that
447 evaporation from *Sphagnum* moss was larger than transpiration of *Sasa* plants on average.
448 Takagi et al. (1999), which is the previous study conducted in the same area of Sarobetsu Mire,
449 reported that the invasion of *Sasa* plants increased ET. Discrepancy between their and our
450 results chiefly arises from methodological difference as described above. We think that our
451 result that *Sasa* plants didn't increase ET is more reliable, because the result arose from
452 continuous flux measurement during four snow-free periods. In addition, larger H at *Sasa* site
453 supports our idea that ET was smaller at *Sasa* site. The reasons of smaller ET at *Sasa* site are
454 restricted evaporation in the early growing season (Table 2, Fig. 3) and stomatal control on G_s
455 (Table 4 and Fig. 5). The former would be caused by leaf litter of *Sasa* plants, which covered
456 the ground surface including *Sphagnum* moss surviving under the shade of vascular plants. In
457 the early growing season, before leaf expansion, the leaf litter mulching restricted evaporation,
458 resulting in smaller ET. Even in the mid-season, when LAI peaked above $3 \text{ m}^2 \text{ m}^{-2}$ (Fig. 2), ET
459 at *Sasa* site didn't exceed ET at *Sphagnum* site, because G_s was still lower at *Sasa* site. Midday
460 G_s of *Sasa* site in the mid-season of 2007-2009 ($< 5 \text{ mm s}^{-1}$) (Fig. 5) was lower than those of
461 other shrub bogs (Humphreys et al., 2006; Lafleur, 2008), which suggests that *Sasa* plants had
462 lower stomatal conductance. A lysimeter experiment in central Hokkaido, northern Japan
463 (Fujimoto et al., 2006) showed a similar result that ET was larger at a *Sphagnum*-dominated

464 bog than a *Sasa*-invaded bog, and the inter-site difference in ET was larger in the early season.
465 Similar results were also reported for peatlands in southern Canada; summer ET was not smaller
466 at a *Sphagnum* bog than wooded fens (Humphreys et al., 2006), and annual ET was larger at an
467 open bog than an adjacent treed bog (Strilesky and Humphreys, 2012), which was attributed to
468 the low transpiration of overstory trees of black spruce.

469 The CV of mean ETs of the four peak growth seasons was only 1.5% at *Sphagnum* site
470 despite unstable meteorological conditions (Table 4), which was much smaller than that of
471 precipitation (35.5%). The low CV of *Sphagnum* ET agreed with a result at boreal bogs, which
472 showed stable ETs despite fluctuated precipitation (Kurbatova et al., 2002), and indicates that
473 *Sphagnum* moss can stabilize evaporation because of its high ability to suck capillary water
474 even in rainless conditions (Price and Whittington, 2010). At *Sasa* site, however, the CV of
475 mean ET was higher at 9.9 % (Table 4), and cumulative ET increased in 2010 by about 25%
476 (Table 3). In 2010, northern Japan experienced an abnormally hot summer with more
477 precipitation (Otomi et al., 2012); air temperature and precipitation were higher or larger than
478 their 30-year normal values by 1.8°C and 172 mm, respectively, in the mid-season (Table 1).
479 As a result, LAI was significantly higher in 2010 than in 2009 (Fig. 2). Higher G_s in 2010 will
480 be caused by higher LAI, whereas such an abnormal summer didn't affect ET at *Sphagnum* site
481 (Table 3). The increase in cumulative ET at *Sasa* site suggests that water consumption by ET
482 will increase at *Sasa*-invaded peatland under the future warming environment through the
483 enhanced growth of *Sasa* plants.

484

485 **5. Conclusions**

486 ET of a peatland dominated by *Sasa* plants, mesic dwarf bamboo, wasn't larger than that of an
487 adjacent *Sphagnum*-dominated bog. This result indicates that the invasion of *Sasa* plants
488 doesn't contribute to further drying of the ombrotrophic bog at present. However, the ETs were

489 almost identical in 2010 with an abnormally hot wet summer, because ET increased by about
490 25% at the *Sasa*-dominated peatland. The increase in ET was most probably caused by higher
491 LAI of *Sasa*, vascular plants, because of the hot wet condition. This result predicts that ET will
492 increase at the *Sasa*-dominated area, if the future warming environment accompanies more
493 precipitation.

494

495 **Acknowledgement**

496 Climate data in Table 1 were downloaded from the website of Japanese Meteorological
497 Agency (<http://www.data.jma.go.jp/obd/stats/etrn/index.php>). This work was financially
498 supported by JSPS KAKENHI (no. 20241002) and Environment Research and Technology
499 Development Fund by the Ministry of the Environment, Japan. We thank Hokkaido Office of
500 Ministry of the Environment, Japan, to permit field work in a special protection zone of Rishiri-
501 Rebun-Sarobetsu National Park, and R. Oshita, who measured LAI.

502

503

504 **References**

- 505 Berg, E.E., Hillman, K.M., Dial, R. and DeRuwe, A., 2009. Recent woody invasion of wetlands on the
506 Kenai Peninsula Lowlands, south-central Alaska: a major regime shift after 18 000 years of
507 wetSphagnum–sedge peat recruitment. *Canadian Journal of Forest Research*, 39(11): 2033-2046.
- 508 Bozkurt, S., Lucisano, M., Moreno, L. and Neretnieks, I., 2001. Peat as a potential analogue for the
509 long-term evolution in landfills. *Earth-Sci Rev*, 53: 95-147.
- 510 Brown, S.M., Petrone, R.M., Mendoza, C. and Devito, K.J., 2010. Surface vegetation controls on
511 evapotranspiration from a sub-humid Western Boreal Plain wetland. *Hydrol Process*, 24(8): 1072-
512 1085.
- 513 Charman, D.J. et al., 2013. Climate-related changes in peatland carbon accumulation during the last
514 millennium. *Biogeosciences*, 10(2): 929-944.
- 515 de Vries, D., 1963. Thermal properties of soils. In: W. van Wijk (Editor), *Physics of Pland Environment*.
516 North-Holland Publishing Co., Amsterdam, pp. 210-235.
- 517 Dorrepaal, E. et al., 2009. Carbon respiration from subsurface peat accelerated by climate warming in
518 the subarctic. *Nature*, 460(7255): 616-619.
- 519 Falge, E. et al., 2001. Gap filling strategies for long term energy flux data sets. *Agr Forest Meteorol*,
520 107: 71-77.
- 521 Farrick, K.K. and Price, J.S., 2009. Ericaceous shrubs on abandoned block-cut peatlands: implications
522 for soil water availability andSphagnumrestoration. *Ecohydrology*, 2(4): 530-540.
- 523 Fenner, N. and Freeman, C., 2011. Drought-unduced carbon loss in peatlands. *Nat Geosci*, 4: 895-900.
- 524 Foken, T. and Wichura, B., 1996. Tools for quality assessment of surface-based flux measurements. *Agr*
525 *Forest Meteorol*, 78: 83-105.
- 526 Frolking, S., Roulet, N. and Fuglestvedt, J., 2006. How northern peatlands influence the Earth's radiative
527 budget: Sustained methane emission versus sustained carbon sequestration. *Journal of Geophysical*
528 *Research*, 111(G1).
- 529 Frolking, S. et al., 2011. Peatlands in the Earth's 21st century climate system. *Environmental Reviews*,
530 19(NA): 371-396.
- 531 Fujimoto, T., Iiyama, I., Sakai, M., Nagata, O. and Hasegawa, S., 2006. Comparison of
532 evapotranspiration between indigenous vegetation and invading vegetation in a bog. *Journal of the*
533 *Japanese Society of Soil Physics*, 103: 39-47.
- 534 Fujimura, Y., Hiroko, F., H., Takada, M. and Inoue, T., 2012. Relationship between hydrology and
535 vegetation change from *Sphagnum* lawns to vascular plant *Sasa* communities. *Landscape and*
536 *Ecological Engineering*, 8(2): 215-221.
- 537 Fujimura, Y., Takada, M., Fujita, H. and Inoue, T., 2013. Change in distribution of the vascular plant
538 *Sasa palmata* in Sarobetsu Mire between 1977 and 2003. *Landscape and Ecological Engineering*,
539 9(2): 305-309.
- 540 Fujita, H., 2006. Lectures on features of peatland and mire vegetation. *Journal of the Japanese Society*

541 of Soil Physics, 104: 97-108.

542 Fujita, H. et al., 2007. An inventory of the mires of Hokkaido, Japan—their development, classification,
543 decline, and conservation. *Plant Ecol*, 200(1): 9-36.

544 Gorham, E., 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic
545 warming. *Ecol Appl*, 1(2).

546 Heikkinen, J.E.P., Virtanen, T., Huttunen, J.T., Elsakov, V. and Martikainen, P.J., 2004. Carbon balance
547 in East European tundra. *Global Biogeochem Cy*, 18(1): n/a-n/a.

548 Hignett, P., 1992. Corrections to temperature measurements with a sonic anemometer. *Bound-Lay*
549 *Meteorol*, 61: 175-187.

550 Hirano, T., Kusin, K., Limin, S. and Osaki, M., 2015. Evapotranspiration of tropical peat swamp forests.
551 *Global Change Biol*, 21.

552 Humphreys, E.R. et al., 2006. Summer carbon dioxide and water vapor fluxes across a range of northern
553 peatlands. *Journal of Geophysical Research*, 111(G4).

554 Iwata, H., Harazono, Y. and Ueyama, M., 2012. Sensitivity and offset changes of a fast-response open-
555 path infrared gas analyzer during long-term observations in an Arctic environment. *Journal of*
556 *Agricultural Meteorology*, 68(3): 175-181.

557 Kellner, E., 2001. Surface energy fluxes and control of evapotranspiration from a Swedish Sphagnum
558 mire. *Agr Forest Meteorol*, 110: 101-123.

559 Kim, J. and Verma, S., 1996. Surface exchange of water vapour between an open Sphgnum fen and the
560 atmosphere. *Bound-Lay Meteorol*, 79: 243-264.

561 Kobayashi, N. et al., 2007. Nighttime transpiration observed over a larch forest in Hokkaido, Japan.
562 *Water Resources Research*, 43(3).

563 Kondo, J., 1976. Heat balance of the East China Sea during the air mass transformation experiment. *J*
564 *Meteorol Soc Jpn*, 54(6): 382-398.

565 Kurbatova, J. et al., 2002. Comparative ecosystem-atmosphere exchange of energy and mass in a
566 European Russian and a central Siberian bog I. Interseasonal and interannual variability of energy
567 and latent heat fluxes during the snowfree period. *Tellus B*, 54B: 497-513.

568 Lafleur, P., 2008. Connecting atmosphere and wetland: energy and water vapour exchange. *Geography*
569 *Compass*, 4(2): 1027-1057.

570 Lafleur, P.M., Hember, R.A., Admiral, S.W. and Roulet, N.T., 2005. Annual and seasonal variability in
571 evapotranspiration and water table at a shrub-covered bog in southern Ontario, Canada. *Hydrol*
572 *Process*, 19(18): 3533-3550.

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

575 Lal, R., 2004. Soil carbon sequestration impacts on global climate change and food security. *Science*,
576 304(5677): 1623-7.

577 Liljedalh, A.K., Hinzman, L.D., Harazono, Y., Zona, D., Tweedie, C.E., Hollister, R.D., Engstrom, R.

578 and Oechel, W.C., 2011. Nonlinear controls on evapotranspiration in arctic coastal wetlands.
579 *Biogeosciences*, 8:3375-3389.

580 Limpens, J. et al., 2008. Peatlands and the carbon cycle: from local processes to global implications - a
581 synthesis. *Biogeosciences*, 5(5): 1475-1491.

582 Mackay, D.S., Ewers, B.E., Cook, B.D. and Davis, K.J., 2007. Environmental drivers of
583 evapotranspiration in a shrub wetland and an upland forest in northern Wisconsin. *Water Resources*
584 *Research*, 43(3): n/a-n/a.

585 Massman, W.J., 2000. A simple method for estimating frequency response corrections for eddy
586 covariance systems. *Agr Forest Meteorol*, 104: 185-198.

587 Mitsch, W.J. et al., 2012. Wetlands, carbon, and climate change. *Landscape Ecology*, 28(4): 583-597.

588 Monteith, J.L., 1965. Evaporation and the environment. *Symposium of the Society of Exploratory*
589 *Biology*, 19: 205-234.

590 Moore, P.A., Pypker, T.G. and Waddington, J.M., 2013. Effect of long-term water table manipulation on
591 peatland evapotranspiration. *Agr Forest Meteorol*, 178-179: 106-119.

592 Murphy, M., Laiho, R. and Moore, T.R., 2009. Effects of Water Table Drawdown on Root Production
593 and Aboveground Biomass in a Boreal Bog. *Ecosystems*, 12(8): 1268-1282.

594 Novick, K.A., Oren, R., Stoy, P.C., Siqueira, M.B.S. and Katul, G.G., 2009. Nocturnal
595 evapotranspiration in eddy-covariance records from three co-located ecosystems in the
596 Southeastern U.S.: Implications for annual fluxes. *Agr Forest Meteorol*, 149(9): 1491-1504.

597 Ohira, A., 1995. Holocene evolution of peatland and paleoenvironmental changes in the Sarobetsu
598 lowland, Hokkaido, northern Japan. *Geographical Review of Japan*, 68: 695-712.

599 Otomi, Y., Tachibana, Y. and Nakamura, T., 2012. A possible cause of the AO polarity reversal from
600 winter to summer in 2010 and its relation to hemispheric extreme summer weather. *Clim Dynam*,
601 40(7-8): 1939-1947.

602 Price, J.S. and Whittington, P.N., 2010. Water flow in Sphagnum hummocks: Mesocosm measurements
603 and modelling. *J Hydrol*, 381(3-4): 333-340.

604 Ryden, H. and Jeglum, J., 2006. *The Biology of Peatlands*. Oxford University Press, New York, 343 pp.

605 Ryu, Y., Baldocchi, D.D., Ma, S. and Hehn, T., 2008. Interannual variability of evapotranspiration and
606 energy exchange over an annual grassland in California. *Journal of Geophysical Research*, 113(D9).

607 Sakaguchi, Y., Kahima, K. and Matsubara, A., 1985. Holocene marine deposits in Hokkaido and their
608 sedimentary environments. *Bulletin of the Department of Geography, University of Tokyo*, 17: 1-
609 17.

610 Shimoyama, K., 2003. Seasonal and interannual variation in water vapor and heat fluxes in a West
611 Siberian continental bog. *Journal of Geophysical Research*, 108(D20).

612 Stoy, P.C. et al., 2013. A data-driven analysis of energy balance closure across FLUXNET research sites:
613 The role of landscape scale heterogeneity. *Agr Forest Meteorol*, 171-172: 137-152.

614 Strilesky, S.L. and Humphreys, E.R., 2012. A comparison of the net ecosystem exchange of carbon

615 dioxide and evapotranspiration for treed and open portions of a temperate peatland. *Agr Forest*
616 *Meteorol*, 153: 45-53.

617 Takada, M. et al., 2012. Geographical assessment of factors for *Sasa* expansion in the Sarobetsu mire,
618 Japan. *Journal of Landscape Ecology*, 5(1): 58-71.

619 Takagi, K., Tsuboya, T., Takahashi, H. and Inoue, T., 1999. Effect of the invasion of vascular plants on
620 heat and water balance in the Sarobetsu mire, northern Japan. *Wetlands*, 19(1): 246-254.

621 Takakuwa, J. and Ito, K., 1986. Ecological aspects of *Sasa* in mires. *Memories of Environmental Science*,
622 Hokkaido University, 2: 47-65.

623 Takami, S., Sakuratani, T. and Horie, T., 2013. Environmental and genotypic effects on stomatal control
624 of evapotranspiration from irrigated rice. *Journal of Agricultural Meteorology*, 69(3): 101-108.

625 Talbot, J., Richard, P.J.H., Roulet, N.T. and Booth, R.K., 2010. Assessing long-term hydrological and
626 ecological responses to drainage in a raised bog using paleoecology and a hydrosequence. *J Veg Sci*,
627 21(1): 143-156.

628 Tsujii, T., 1963. Reports on the undeveloped peatland in Hokkaido, Hokkaido Development Agency,
629 Tokyo.

630 Twine, T.E. et al., 2000. Correcting eddy-covariance flux underestimates over a grassland. *Agr Forest*
631 *Meteorol*, 103(279-300): 279.

632 Vickers, D. and Mahrt, L., 1997. Quality control and flux sampling problems for tower and aircraft data.
633 *J Atmos Ocean Tech*, 14: 512-526.

634 Waddington, J.M. et al., 2015. Hydrological feedbacks in northern peatlands. *Ecohydrology*, 8(1): 113-
635 127.

636 Walker, M.D. et al., 2006. Plant community responses to experimental warming across the tundra biome.
637 *Proc Natl Acad Sci U S A*, 103(5): 1342-6.

638 Ward, S.E. et al., 2013. Warming effects on greenhouse gas fluxes in peatlands are modulated by
639 vegetation composition. *Ecol Lett*, 16(10): 1285-93.

640 Webb, E.K., Pearman, G.I. and Leuning, R., 1980. Correction of flux measurements for density effects
641 due to heat and water vapor transfer. *Q J Roy Meteor Soc*, 106: 85-106.

642 Wilczak, J.M., Oncley, S.P. and Stage, S.A., 2001. Sonic anemometer tilt correction algorithms. *Bound-*
643 *Lay Meteorol*, 106: 85-106.

644 Wilson, K. et al., 2002. Energy balance closure at FLUXNET sites. *Agr Forest Meteorol*, 113(223-243):
645 223.

646 Wu, J., Kutzbach, L., Jager, D., Wille, C. and Wilkening, M., 2010. Evapotranspiration dynamics in a
647 boreal peatland and its impact on the water and energy balance. *Journal of Geophysical Research*,
648 115(G4).

649 Yabe, K. and Uemura, S., 2001. Variation in size and shape of *Sphagnum* hummocks in relation to
650 climatic conditions in Hokkaido Island, northern Japan. *Canadian Journal of Botany*, 79(11): 1318-
651 1326.

- 652 Yazaki, T., Urano, S.-i. and Yabe, K., 2006. Water balance and water movement in unsaturated zones of
653 Sphagnum hummocks in Fuhrengawa Mire, Hokkaido, Japan. *J Hydrol*, 319(1-4): 312-327.
- 654 Yazaki, T. and Yabe, K., 2012. Effects of snow-load and shading by vascular plants on the vertical
655 growth of hummocks formed by *Sphagnum papillosum* in a mire of northern Japan. *Plant Ecol*,
656 213(7): 1055-1067.
- 657 Yu, Z.C., 2012. Northern peatland carbon stocks and dynamics: a review. *Biogeosciences*, 9(10): 4071-
658 4085.
- 659 Zhou, L., Zhou, G., Liu, S. and Sui, X., 2010. Seasonal contribution and interannual variation of
660 evapotranspiration over a reed marsh (*Phragmites australis*) in Northeast China from 3-year eddy
661 covariance data. *Hydrol Process*, 24(8): 1039-1047.
- 662
- 663

664 **Legends of figures**

665 **Fig. 1.** Seasonal variations in daily values of groundwater level (GWL) (a-d), soil water content
666 (SWC) at 10-cm depth (e-h) gap-filled evapotranspiration (ET) (i-l) and cumulative ET
667 (m-p) during the snow-free period at *Sphagnum* and *Sasa* sites in 2007, 2008, 2009 and
668 2010.

669

670 **Fig. 2.** Seasonal variations in leaf area index (LAI) at *Sasa* site. Error bars denote 1 standard
671 error ($n = 70$). * denotes significant difference between 2009 and 2010 in the same
672 month at a significant level of 0.01 according to Student's *t*-test.

673

674 **Fig. 3.** Diurnal variations in net radiation (R_n) (a-c), soil heat flux at the ground surface (G) (d-
675 f), sensible heat flux (H) (g-i) and latent heat flux (LE) (j-l) at *Sphagnum* and *Sasa* sites
676 in the early (May-June), mid- (July-August) and late (September-October) growing
677 seasons. Data are ensemble means of half-hourly measured data.

678

679 **Fig. 4.** Seasonal variations in monthly means of nighttime evapotranspiration (ET_{night}) (a), the
680 ratio of nighttime and daytime ETs ($ET_{\text{night}} / ET_{\text{day}}$) (b) and nighttime vapor pressure
681 deficit (VPD) and wind velocity (WV) (c) at *Sphagnum* and *Sasa* sites from May through
682 October. Error bars in (a) and (c) denote 1 standard error.

683

684 **Fig. 5.** Diurnal variations in bulk surface conductance in dry conditions (dry G_s) at *Sphagnum*
685 and *Sasa* sites in the early (May-June), mid- (July-August) and late (September-
686 October) growing seasons in 2007-2009 and 2010. Data are ensemble means of half-
687 hourly measured data. Error bars demote 1 standard error.

688

689 **Fig. 6.** Relationships between daytime (800-1600) bulk surface conductance in dry conditions
690 (dry G_s) and vapor pressure deficit (VPD) at *Sphagnum* and *Sasa* sites in the mid-season
691 (July-August) in 2007-2009 and 2010. Half-hourly measured data are classified by
692 groundwater level (GWL) into two groups with equal quantities. The median GWL is
693 shown in each figure. Circles are binned averages of deciles according to VPD. Error
694 bars denote 1 standard error.

695

696 **Fig. 7.** Relationships between daytime (800-1600) bulk surface conductance in dry conditions
697 (dry G_s) and groundwater level (GWL) in the mid-growing season (July-August). The
698 range of vapor pressure deficit (VPD) is limited between 2 and 8 hPa at *Sphagnum* site
699 (a) and between 3 and 7 hPa at *Sasa* site (b) to avoid the effect of VPD (Fig. 6). Half-
700 hourly measured data are plotted, and a line is fitted ($p < 0.05$).

701

702
703
704

Table 1. Air temperature and precipitation measured at Toyotomi meteorological observatory. Their normal values for 30 years until 2010 and anomalies in 2007-2010 are shown.

Year	Air temperature (°C)				Precipitation (mm)			
	May-Jun.	Jul.-Aug.	Sep.-Oct.	May-Oct.	May-Jun.	Jul.-Aug.	Sep.-Oct.	May-Oct.
Normal	11.4	18.6	12.6	14.2	115	214	278	607
2007	0.65	0.35	0.35	0.45	-33	-51	-42	-126
2008	-0.65	-0.20	0.7	-0.05	3	-80	-118	-195
2009	0.45	-1.55	0.00	-0.37	61	21	-92	-9
2010	0.50	1.75	0.80	1.02	-10	172	-11	152

705

706 **Table 2.** Measured values at around midday (1000-1400) of air temperature (T_a), water vapor pressure deficit (VPD), net radiation (R_n), soil heat
707 flux at the ground surface (G), sensible heat flux (H), latent heat flux (LE), Bowen ratio (β), bulk aerodynamic conductance (G_a), bulk
708 surface conductance (G_s) and G_s in dry conditions (dry G_s), and daily values of gap-filled evapotranspiration (ET), potential ET (PET) and
709 the ratio of ET and PET (PE / PET) (mean \pm 1 standard error) at *Sphagnum* and *Sasa* sites in the early (May-June), mid- (July–August) and
710 late (September-October) growing seasons.

711

Site	Season	T_a	VPD	R_n	G	H	LE	β	G_a	G_s	Dry G_s	ET	PET	ET / PET
		°C	hPa	W m ⁻²	W m ⁻²	W m ⁻²	W m ⁻²			mm s ⁻¹	mm s ⁻¹	mm s ⁻¹	mm d ⁻¹	mm d ⁻¹
<i>Sphagnum</i>	May-Jun.	16.2±0.11a	4.61±0.09a	420±5a	30.0±0.6a	176±3a	151±2a	1.17	27.5±0.3a	6.36±0.13a	5.73±0.10a	1.91±0.05b	4.02±0.14a	0.48
	Jul.-Aug.	21.4±0.06c	5.27±0.09b	377±4b	25.4±0.5b	114±2b	170±2c	0.67	25.0±0.2b	6.07±0.10a	5.88±0.09a	2.13±0.05a	3.79±0.11a	0.56
	Sep.-Oct.	17.5±0.12b	6.78±0.08c	309±3c	21.1±0.6c	107±2c	130±2b	0.82	25.4±0.2b	5.07±0.09b	4.78±0.09b	1.71±0.04c	3.38±0.11b	0.51
<i>Sasa</i>	May-Jun.	15.7±0.11a	5.20±0.10a	412±5a	22.8±0.4a	200±3a	104±1a	1.92	29.7±0.3a	4.28±0.09a	3.74±0.07a	1.45±0.04c	4.38±0.15a	0.33
	Jul.-Aug.	21.5±0.07b	6.27±0.09b	369±4b	14.1±0.2b	136±2b	153±2c	0.89	24.4±0.3b	4.69±0.09b	4.39±0.08b	1.93±0.04a	4.16±0.12a	0.46
	Sep.-Oct.	17.2±0.11c	6.70±0.08c	296±3c	6.0±0.2c	102±2c	128±2b	0.80	23.3±0.3c	4.32±0.10a	3.76±0.06a	1.61±0.04b	3.36±0.13b	0.48

712

713 * Different letters in each column for each site denote significant difference among the seasons at significant level of 0.05 according to Tukey's HSD, after
714 ANOVA ($p < 0.01$).

715

716 **Table 3.** Cumulative evapotranspiration (mm) for 201 days from April 21 to November 7.
 717 Figures in parentheses are cumulation for 147 days from April 21 to September 15.
 718

Year	<i>Sphagnum</i>	<i>Sasa</i>	Precipitation
2008	362	300	442
2009	381 (298)	(234)	615 (474)
2010	374	372	810
Mean±1 SD	372±8	-	622±150

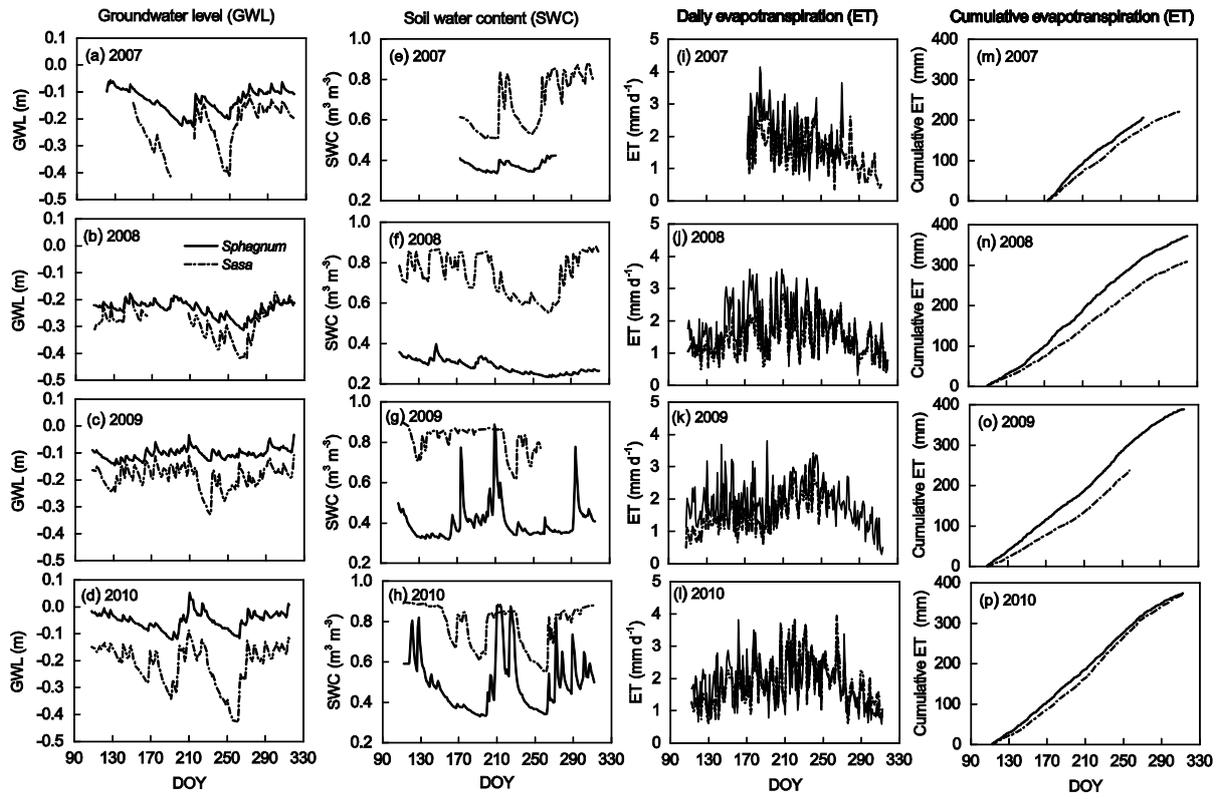
719

720 **Table 4.** Mean or cumulative values of precipitation (P), air temperature (T_a), midday (1000-1400) vapor pressure deficit (VPD), soil water content
721 (SWC), net radiation (R_n), gap-filled sensible heat flux (H), gap-filled latent heat flux (LE), Bowen ratio (β), midday bulk surface
722 conductance (G_s), midday G_s in dry conditions (dry G_s), gap-filled evapotranspiration (ET), potential ET (PET) (mean \pm 1 standard error)
723 and the ratio of ET and PET (ET /PET) at *Sphagnum* and *Sasa* sites during the common measurement period of 86 days from late June
724 through mid-September.
725

Year	Site	P	T_a	Midday VPD	SWC	R_n	H	LE	β	Midday G_a	Midday dry G_s	ET	PET	ET/PET
		mm	°C	hPa	$m^3 m^{-3}$	$MJ m^{-2} d^{-1}$	$MJ m^{-2} d^{-1}$	$MJ m^{-2} d^{-1}$	$MJ m^{-2} d^{-1}$		$mm d^{-1}$	$mm s^{-1}$	$mm d^{-1}$	$mm d^{-1}$
2007	<i>Sphagnum</i>	238	18.4 \pm 0.30	6.0 \pm 0.05	0.37 \pm 0.002	10.5 \pm 0.51	2.55 \pm 0.22	5.14 \pm 0.21	0.43 \pm 0.03	23.5 \pm 1.1	4.97 \pm 0.18	2.09 \pm 0.09	3.92 \pm 0.20	0.53
	<i>Sasa</i>			6.8 \pm 0.05	0.59 \pm 0.009	10.5 \pm 0.50	3.01 \pm 0.28	4.50 \pm 0.16	0.59 \pm 0.05	26.8 \pm 1.5	3.47 \pm 0.08	1.83 \pm 0.06	4.10 \pm 0.22	0.45
2008	<i>Sphagnum</i>	158	18.0 \pm 0.31	6.4 \pm 0.05	0.28 \pm 0.003	10.9 \pm 0.55	3.21 \pm 0.24	5.33 \pm 0.21	0.55 \pm 0.03	24.3 \pm 1.1	5.04 \pm 0.14	2.17 \pm 0.09	4.11 \pm 0.21	0.53
	<i>Sasa</i>			7.4 \pm 0.04	0.70 \pm 0.010	10.2 \pm 0.50	3.29 \pm 0.29	4.36 \pm 0.16	0.68 \pm 0.06	23.2 \pm 1.2	3.89 \pm 0.09	1.77 \pm 0.07	4.25 \pm 0.21	0.42
2009	<i>Sphagnum</i>	327	16.9 \pm 0.26	5.2 \pm 0.04	0.43 \pm 0.012	10.5 \pm 0.44	2.28 \pm 0.17	5.28 \pm 0.18	0.41 \pm 0.03	25.4 \pm 0.8	6.00 \pm 0.12	2.15 \pm 0.07	3.86 \pm 0.18	0.56
	<i>Sasa</i>			6.5 \pm 0.04	0.81 \pm 0.008	10.1 \pm 0.41	2.65 \pm 0.21	4.48 \pm 0.15	0.58 \pm 0.05	26.9 \pm 1.3	4.08 \pm 0.08	1.82 \pm 0.06	4.30 \pm 0.19	0.42
2010	<i>Sphagnum</i>	434	20.2 \pm 0.25	4.9 \pm 0.04	0.48 \pm 0.019	10.0 \pm 0.44	2.31 \pm 0.18	5.29 \pm 0.19	0.39 \pm 0.02	26.8 \pm 1.0	6.26 \pm 0.12	2.16 \pm 0.08	3.72 \pm 0.18	0.58
	<i>Sasa</i>			5.6 \pm 0.04	0.73 \pm 0.011	10.0 \pm 0.43	2.58 \pm 0.19	5.50 \pm 0.19	0.45 \pm 0.04	33.5 \pm 1.8	5.81 \pm 0.11	2.24 \pm 0.08	4.33 \pm 0.19	0.52
ANOVA	Site	-	-	**	**	ns	*	**	**	**	**	**	*	-
	Year	-	**	**	**	ns	**	**	**	**	**	**	ns	-
	Interaction	-	-	ns	ns	ns	ns	**	ns	*	**	**	ns	-

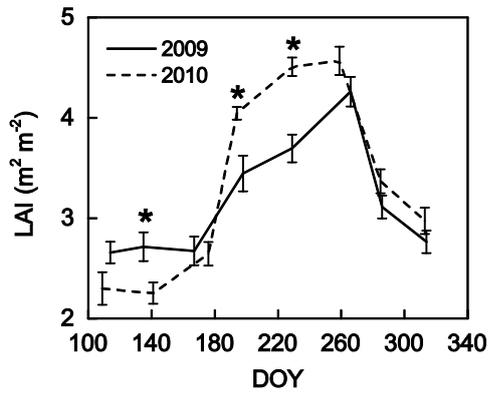
726

727 * Two-way repeated measure ANOVA was applied. **, * and ns denote significance levels of <0.01, <0.05 and > 0.05, respectively.

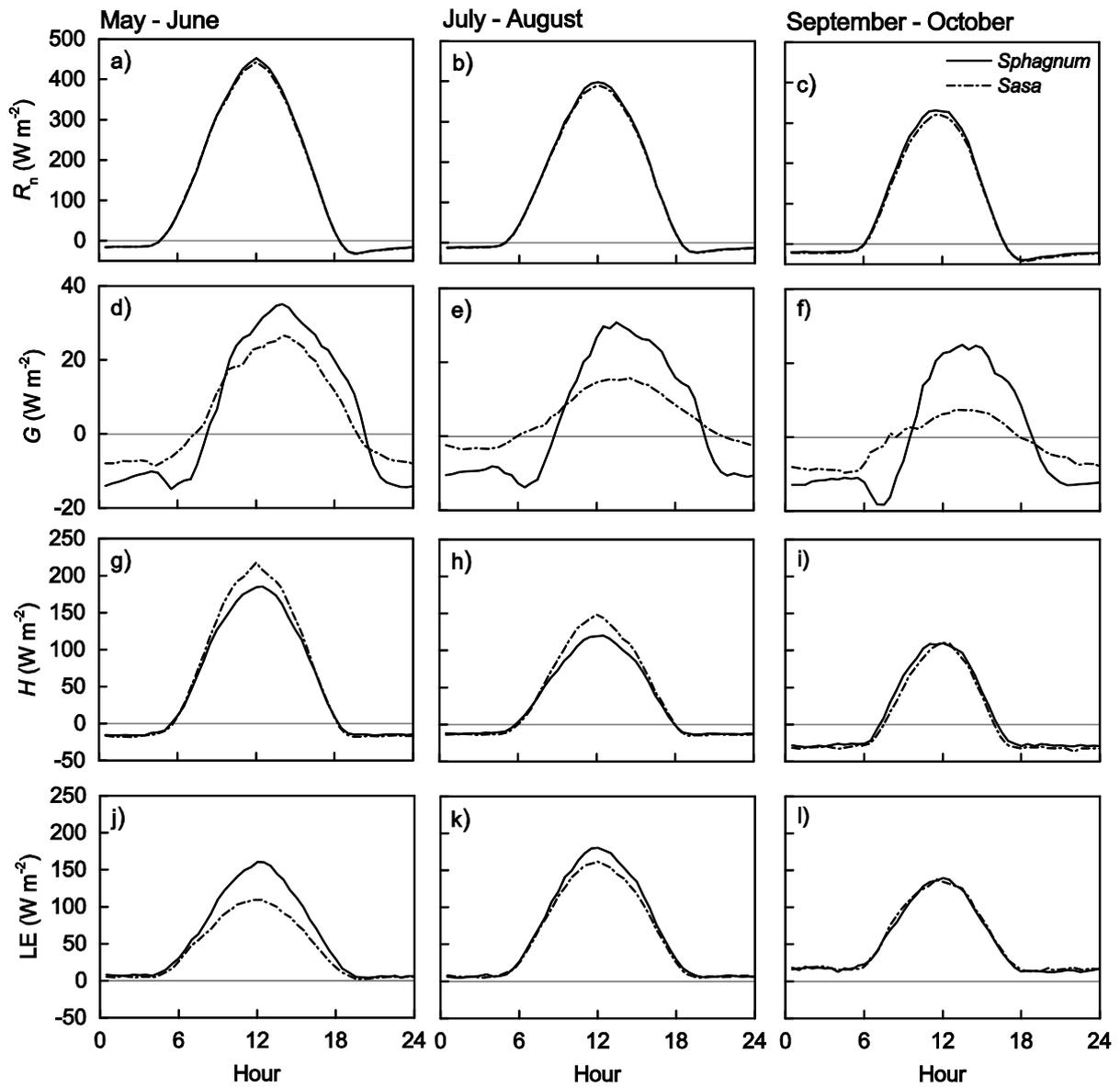


731 Fig. 2

732

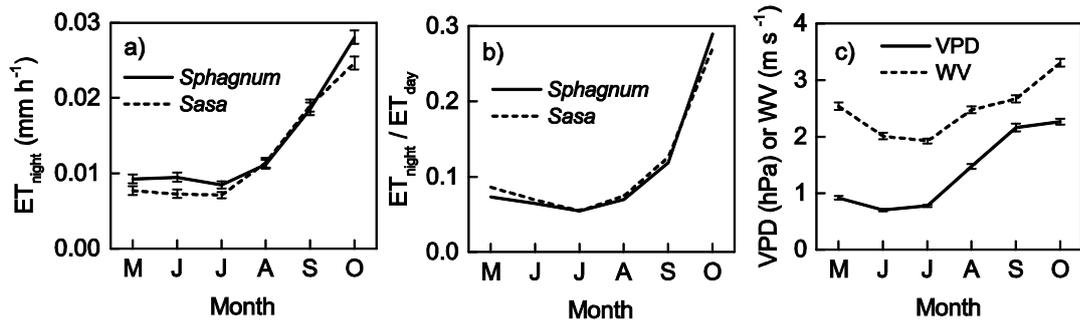


733



737 Fig. 4

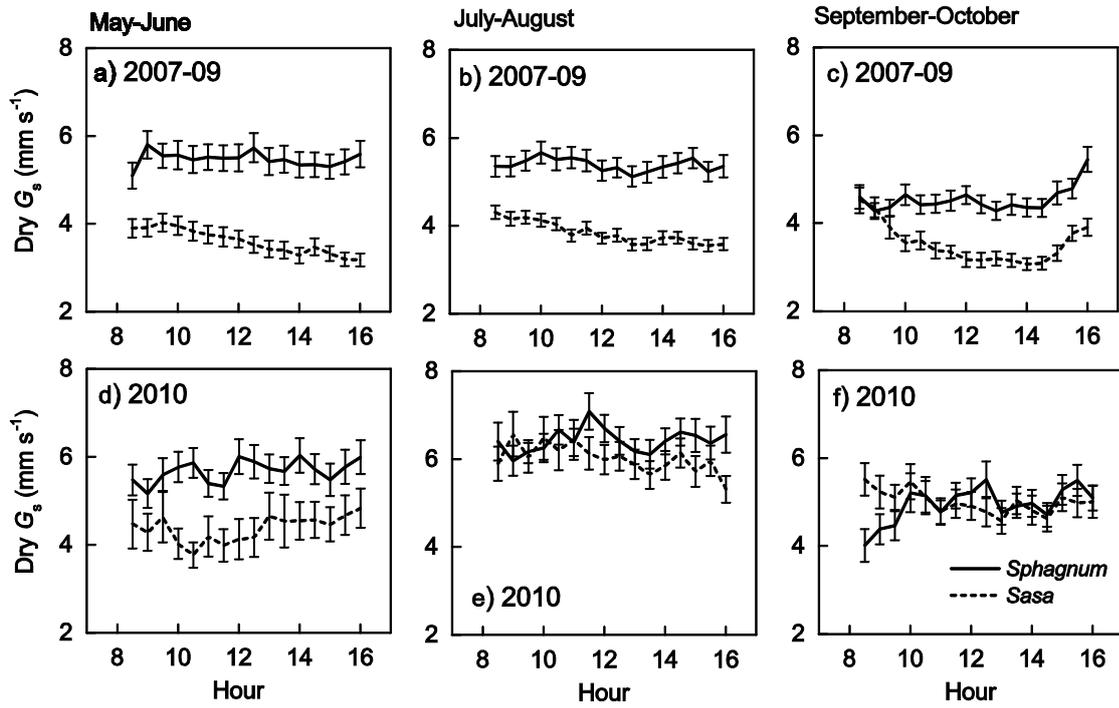
738



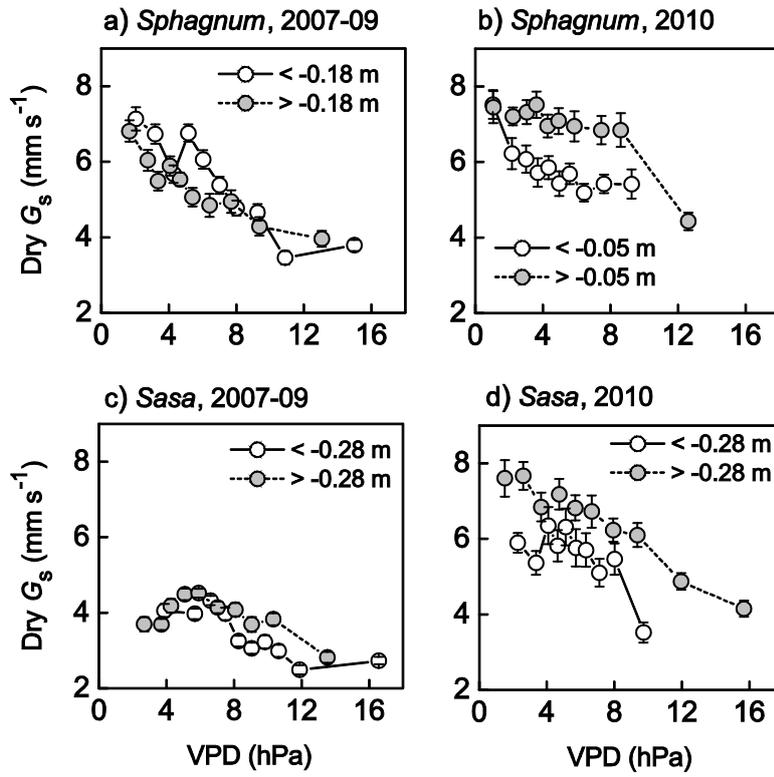
739

740 Fig. 5

741

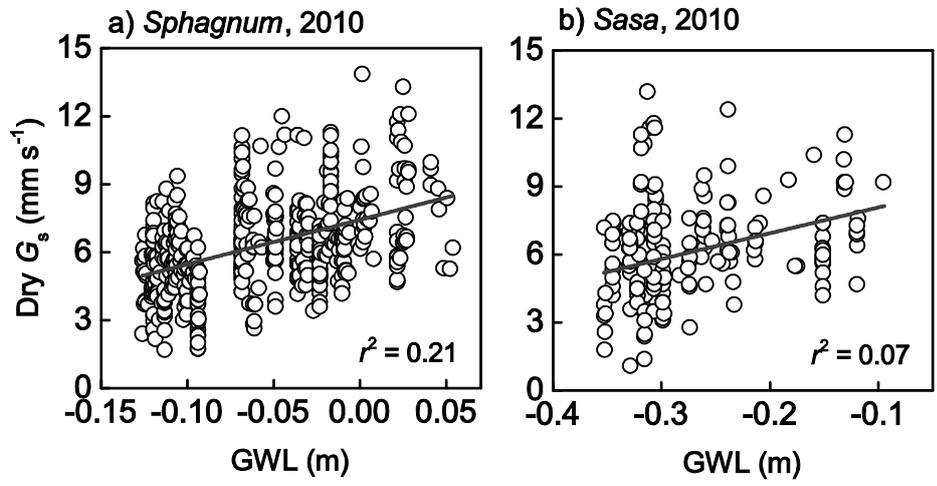


742



746 Fig. 7

747



748