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

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Abstract

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

Keywords

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

1. Introduction

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

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

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

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

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

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

2. Materials and methods

2.1. Study area

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

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

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

2.2. Field measurement

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

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

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

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

Leaf area index (LAI) was measured monthly from April through November in 2009 and 2010 at *Sasa* site. At 70 points within 20 m from the mast, LAI was measured with a plant canopy analyzer (LAI2000; LICOR Inc.) with five replications. LAI of vascular plants above *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 ($= 1800 \text{ s}$), C_s , C_w and C_g are heat capacities of solid ($= 2.5 \times 10^6$), liquid ($=$
185 4.2×10^6) and gas ($= 1.2 \times 10^3$) ($\text{J m}^{-3} \text{K}^{-1}$) (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*).

2.4. Quality control and gap filling of flux data

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

2.5. Energy imbalance

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

2.6. Calculation of bulk surface conductance

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

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

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

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

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

where κ is von Karman constant ($=0.4$), u^* is friction velocity (m s^{-1}), dh is thermal diffusivity, dv is molecular diffusivity of water vapor and u is mean wind velocity (m s^{-1}). The ratio of dh 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 was excluded if there was antecedent precipitation within six hours. Potential ET (PET) was calculated by setting G_s infinite in the PM equation.

3. Results

3.1 Environmental and vegetative conditions

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

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

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

3.2. Energy fluxes and evapotranspiration

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

site.

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

3.3. Interannual variation in evapotranspiration

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

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

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

3.4. Nighttime evapotranspiration

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

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

3.5. Control on evapotranspiration

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

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

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

4. Discussion

4.1. Comparison of ET with other studies

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

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

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

4.2. Seasonal variations

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

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

4.3. Nighttime evapotranspiration

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

4.4. Control on evapotranspiration

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

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

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

4.5. Effects of *Sasa* invasion

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

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

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

5. Conclusions

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

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

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Legends of figures

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

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

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

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

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

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

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

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
Anomaly	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

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 flux at the ground surface (G), sensible heat flux (H), latent heat flux (LE), Bowen ratio (β), bulk aerodynamic conductance (G_a), bulk 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 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 late (September-October) growing seasons.

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

* 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 ANOVA ($p < 0.01$).

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

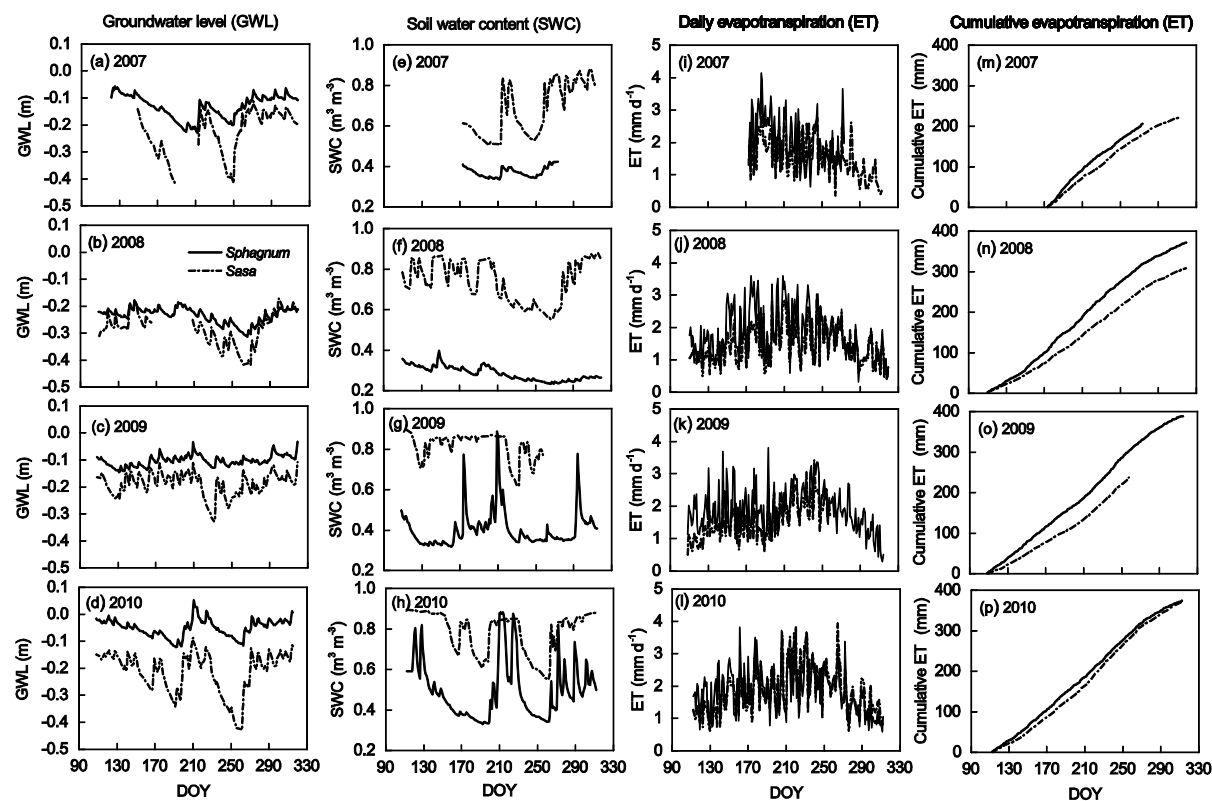
Year	<i>Sphagnum</i>	<i>Sasa</i>	Precipitation
2008	362	300	442
2009	381 (298)	(234)	615 (474)
2010	374	372	810
Mean±1 SD	372±8	-	622±150

Table 4. Mean or cumulative values of precipitation (P), air temperature (T_a), midday (1000-1400) vapor pressure deficit (VPD), soil water content (SWC), net radiation (R_n), gap-filled sensible heat flux (H), gap-filled latent heat flux (LE), Bowen ratio (β), midday bulk surface conductance (G_s), midday G_s in dry conditions (dry G_s), gap-filled evapotranspiration (ET), potential ET (PET) (mean $\pm$ 1 standard error) 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 through mid-September.

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

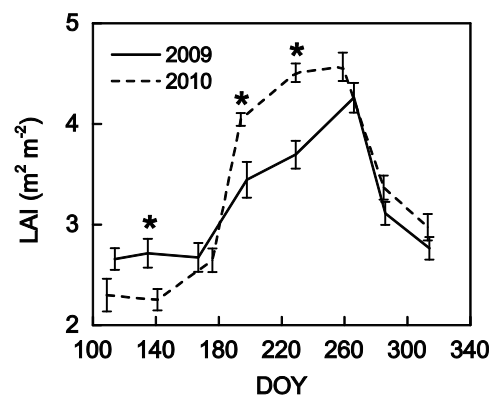
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727 * Two-way repeated measure ANOVA was applied. **, * and ns denote significance levels of <0.01, <0.05 and > 0.05, respectively.



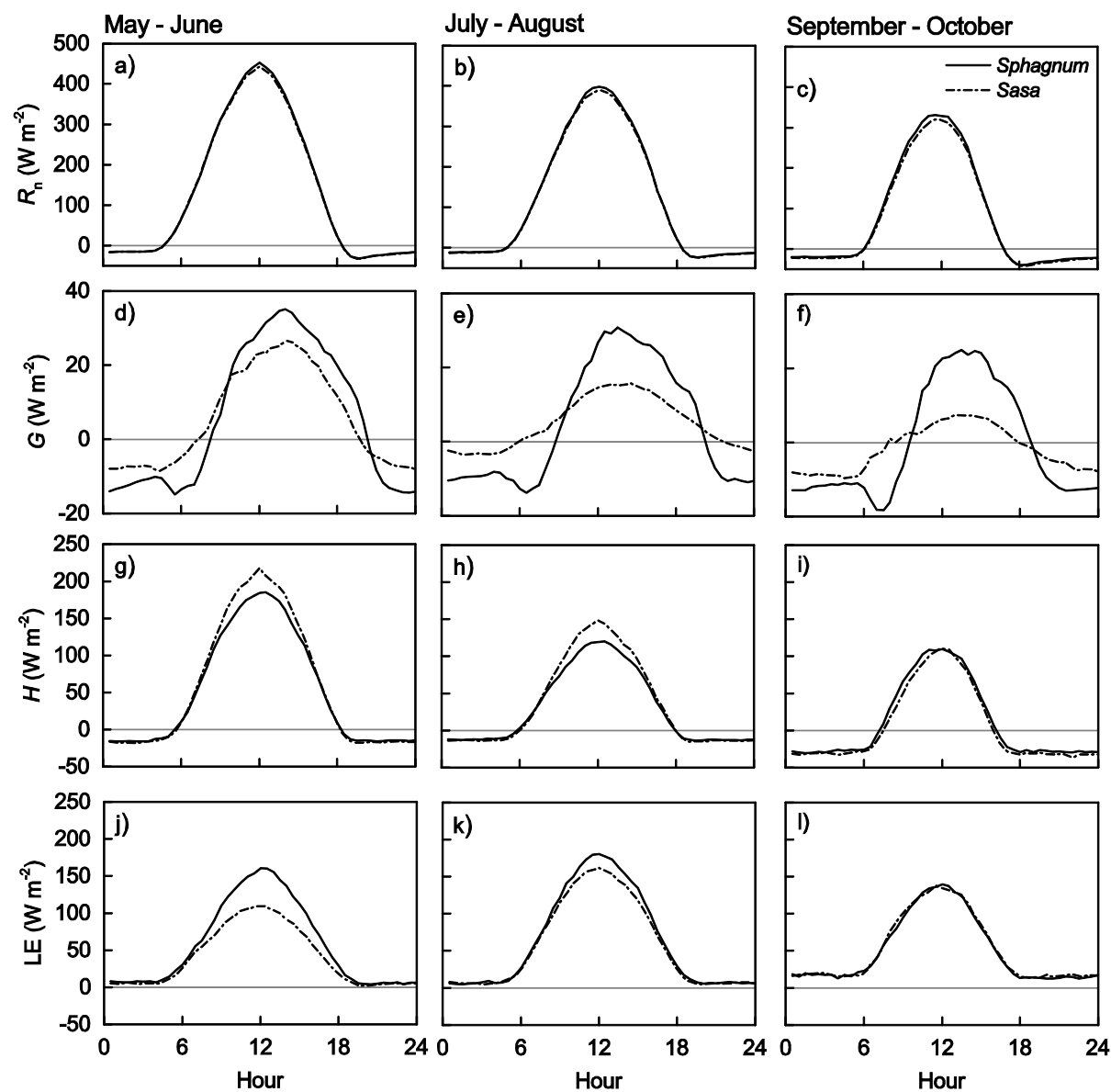
731 Fig. 2

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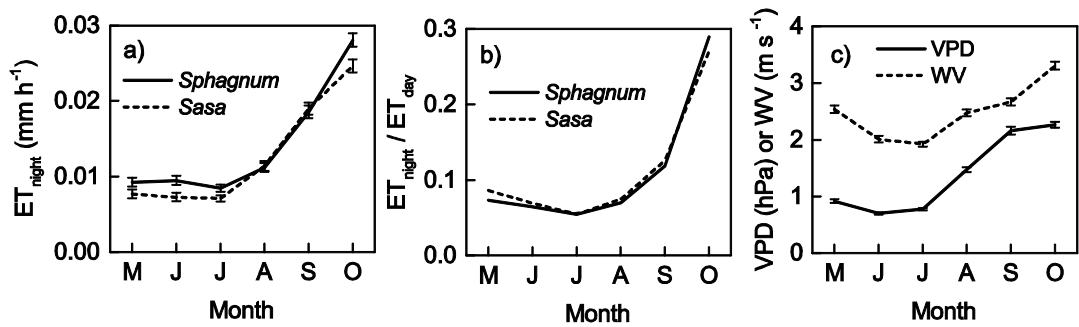
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734 Fig. 3
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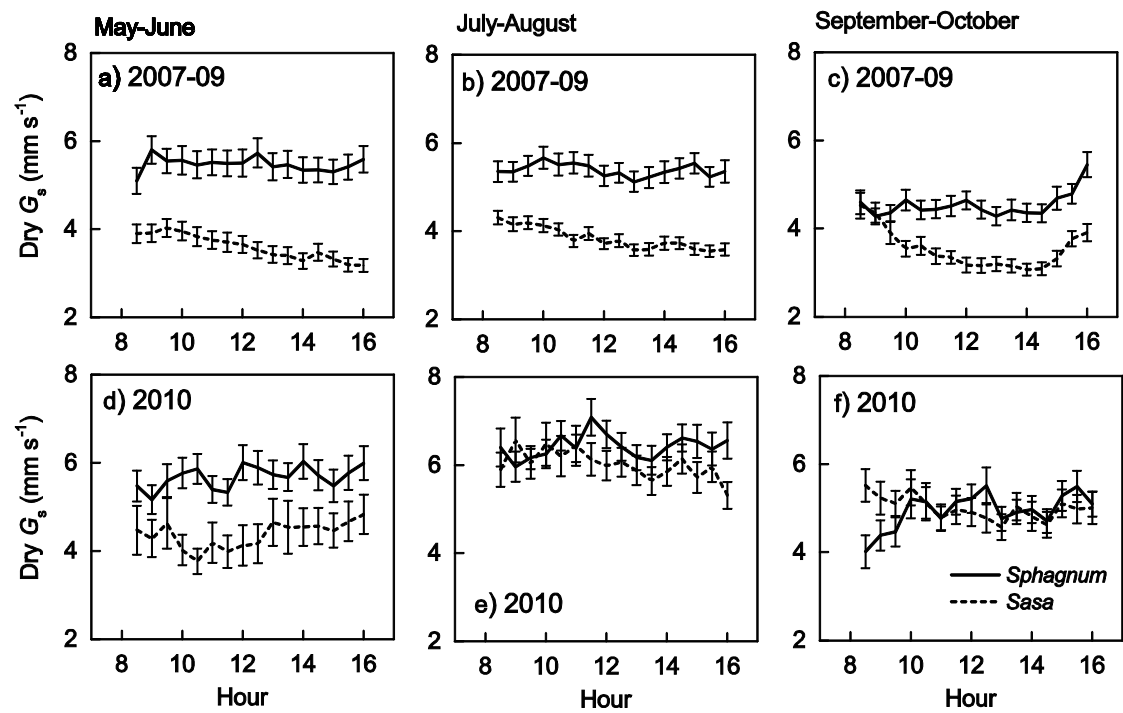
737 Fig. 4

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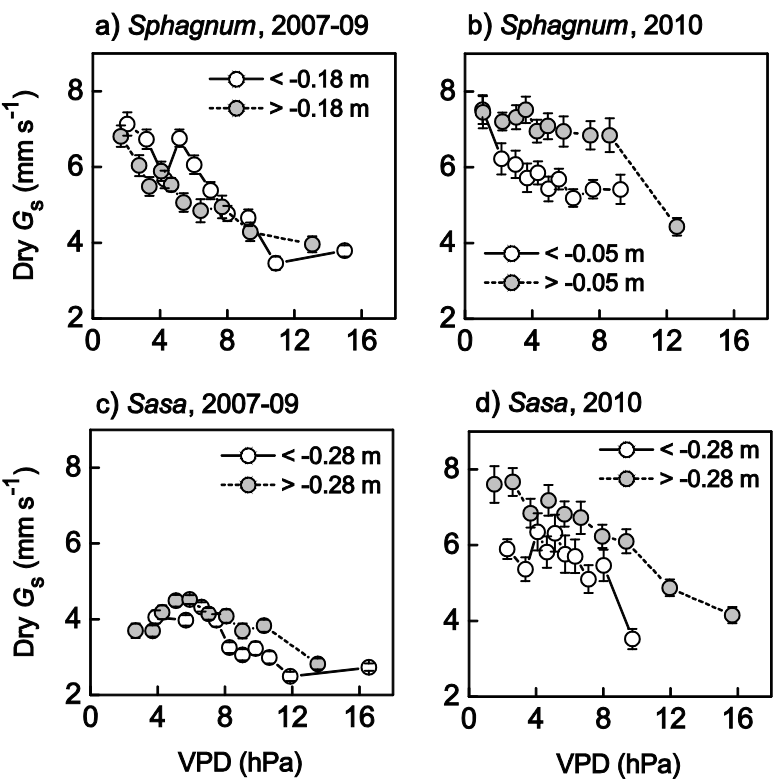


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740 Fig. 5
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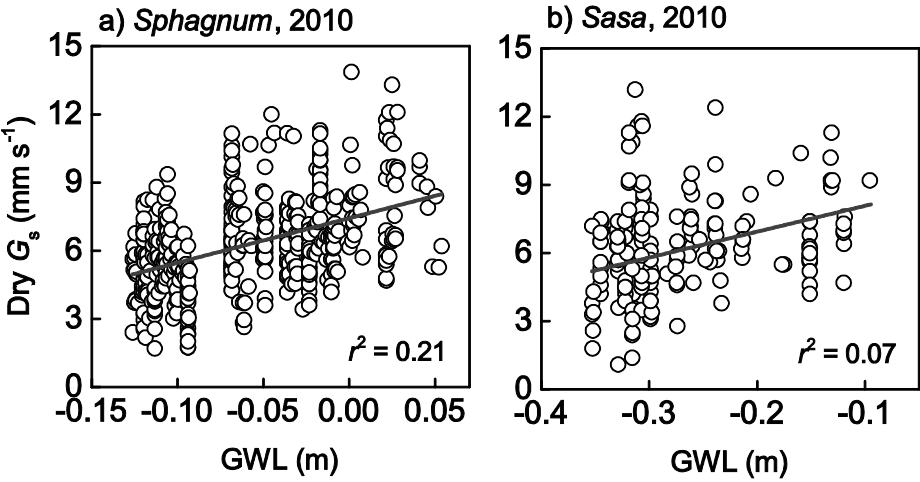


743 Fig. 6
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746 Fig. 7
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