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Temperature Dependency of Photosynthesis of *Sphagnum* spp. Distributed in the Warm-Temperate and the Cool-Temperate Mires of Japan

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ABSTRACT

We investigated the temperature dependency of photosynthetic rates for five Sphagnum species: Sphagnum palustre, S. fimbriatum in the Tadewara mire (south-western Japan in a warm-temperate zone) and S. papillosum, S. fuscum, S. fallax in the East Ochiishi mire (north-eastern Japan in a cool-temperate zone) measuring photosynthetic light response within a temperature range between 5 and 40°C. The maximum photosynthetic rate was obtained at T = 35°C for S. palustre, S. fuscum and S. papillosum, and at T = 30°C for S. fimbriatum and S. fallax. Photosynthetic rates of all these species showed a maximum at 300 - 500 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of PPFD and it decreased at higher PPFD (>500 $\mu mol \cdot m^{-2} \cdot s^{-1}$) under low temperature (5°C - 10°C). These results imply that Sphagnum species are not fully physiologically adapted to low temperature environments, although Sphagnum species distribute mostly in the circumpolar region.

Keywords: *Carbon Dioxide Exchange, Photosynthesis, Sphagnum, Temperature Dependence*

1. Introduction

Carbon accumulation by peat-forming plants is a great concern for the global carbon cycle [1,2]. *Sphagnum* plants are major components of vegetation in boreal mires and form thick peat layers containing huge amounts of organic carbon. Decomposition of peat causes the emission of carbon into the atmosphere, whereas deposition of peat promotes accumulation of carbon in the soil. In addition, the balance of peat formation and decomposition controls net carbon flow between the rhizosphere and the atmosphere.

The growth and primary productivity of *Sphagnum* spp. have been investigated under different conditions of water deficiency, nutrition, acidity, temperature, UV radiation and atmospheric pollution from pollutants such as ozone or bisulphate. Prior eco-physiological studies of *Sphagnum* plants clarified that most of the *Sphagnum* spp. grow well under acidic and poor nutritional conditions [3,4]. *Sphagnum* spp. are acidophilic species and the plants change the habitat acidity by exchanging soluble cations with protons at the cell walls of the plants. Only some few species such as *S. squarrosum* and *S. fim-*

briatum can colonize under calcareous conditions [5]. Colonization of these pioneer *Sphagnum* spp. acidifies the habitat and then other species are able to colonize the acidic habitat. The growth of *Sphagnum* declined in growth media with high nutrient concentrations, especially those containing high levels of inorganic phosphorus [4].

Although the growth responses of *Sphagnum* plants to various environmental parameters have already been investigated, physiological responses of *Sphagnum* spp. such as photosynthetic activity have not been fully investigated. The water availability of habitats or the water contents of plants are among the limiting factors of the photosynthetic activity of *Sphagnum* [6-8]. Many *Sphagnum* spp. have optimal water contents for photosynthesis at 600% - 800% of dry weight and the photosynthetic rate rapidly decreases when the water content becomes lower than the optimal. Desiccation tolerance of *Sphagnum* plants can be evaluated by the minimum water content in plants that maintain photosynthetic activity and the duration of dehydration from which the plants can recover physiological activity after rehydration [9,10].

Desiccation tolerance depends on the species and it determines the distribution of *Sphagnum* species along the gradients of microtopography within a mire community [3]. Hummock-forming species have a high tolerance for desiccation. *Sphagnum* spp. in section Acutifolia have high desiccation tolerance because the green cells face the adaxial surface and in addition the green cells are covered with hyaline cells which face the abaxial surface. Species growing on hollow or submerged species are poorly adapted to dry conditions, although the species can survive under dry conditions for a short period. *Sphagnum* spp. in section Cuspidata have low desiccation tolerance because of their leaf anatomical structure is the opposite of that found in species in section Acutifolia.

Recent studies on the relationship between *Sphagnum* growth and nutrition have been focused on atmospheric nitrogen deposition [11-16] and many studies showed that enhanced nitrogen deposition accelerates the photosynthetic rate of *Sphagnum* plants, whereas growth of plants was limited by the deposition of atmospheric nitrogen.

Effects of environmental pollutants on the photosynthesis of *Sphagnum* plants have also been of great concern. Bisulphite (HSO_3^-) in the atmospheric deposition has an extremely inhibiting effect on *Sphagnum* photosynthesis [17-19], and 5.0 mM of HSO_3^- has a completely fatal effect on *Sphagnum*. Iron deposition accompanying bisulphite deposition from the atmosphere decreases the effect of bisulphite on *Sphagnum*, and thus plants growing in polluted areas have higher tolerance capability for atmospheric pollution [20].

Ozone also has an inhibiting effect on the photosynthesis of *Sphagnum* plants. *Sphagnum* elongation and photosynthetic rate declined after 6 - 9 weeks of O_3 exposure at 70 - 80 ppb [21]. Respiration rate of *Sphagnum* plants increased after exposure to O_3, although the photosynthetic rate was not affected by O_3 exposure [21,22].

Increased UV-B radiation inhibited elongation and dark respiration, but the effect of UV-B radiation increase on net photosynthetic rate per unit dry weight of plants was not significant [23]. Reduction of solar UV-B increased height growth but decreased volumetric density in *S. magellanicum*; furthermore, UV-B reduction had little effect on biomass production [24,25].

In addition to the effects of environmental pollution and UV radiation, global environmental change's influence on the photosynthetic activity of *Sphagnum* plants is also of great concern because the growth and decomposition of senescent plant materials determine the accumulation rate of organic carbon in peat soil and the consequent global carbon balance. As for the photosynthetic capacity of individual *Sphagnum* plants, the response of growth and photosynthetic rate to the temperature regime has been investigated by various researchers. Investigation on the growth of *S. fuscum*, *S. balticum*, *S. cuspidatum* and *S. magellanicum* under different temperature conditions ranging from T = 11.2°C to 21.4°C, and all of these *Sphagnum* plants showed maximum growth at T = 21.4°C [26]. Temperature dependence of *Sphagnum* photosynthetic rates by using experimental measurement data as well as a theoretical model showed that maximum net photosynthetic rate along a particular temperature regime differed according to light intensity [27]. The optimal temperature in low light intensity conditions (PPFD = 20 μmol·m^{-2}·s^{-1}) was T = 0°C to 5°C, whereas in high light intensity conditions (PPFD = 500 μmol·m^{-2}·s^{-1}) the optimal temperature was between 20°C and 25°C. These studies show that the photosynthetic capacity of *Sphagnum* plants has a rather high optimal temperature range at 20°C to 25°C, even though *Sphagnum* plants successfully distribute in the circumpolar region.

In this paper we investigated the temperature dependence of the carbon assimilation rate of five *Sphagnum* species growing in warm-temperate and cool-temperate zones in Japan. We measured the response of the CO_2 exchange rate of the *Sphagnum* species along a temperature range of 5°C - 40°C, a much wider range compared to those previously reported. Furthermore, we tried to test the hypothesis that *Sphagnum* species can tolerate higher temperature conditions than those in their native distribution areas. We also tried to clarify the differences in temperature dependence for the photosynthetic rates found among various species and climatic zones. Measuring optimum temperatures for photosynthetic rates and making interspecific comparisons provided information on the adaptation of *Sphagnum* plants to low temperature environments. Additionally, we discussed the adaptive traits of *Sphagnum* species and the responses of community structure to global climatic change.

2. Materials and Methods

2.1. Plant Materials

Sphagnum samples were collected from the Tadewara mire in south-western Japan (33.07°N, 131.14°E, 1000 m a.s.l.) in June 2007, and the East Ochiishi mire in northeastern Japan (43.16°N, 145.50°E, 50 m a.s.l.) in September 2007.

The Tadewara mire (measuring 1.0 km east to west, and 3.0 km north to south) is located within the Kujyu volcanic mountain area at 1000 m a.s.l. The mire developed on the gentle slope at the end an alluvial fan. Annual mean temperature in the mire was 9.1°C, average daily maximum temperature was 25.6°C in August, av-

erage daily minimum temperature was –6.2˚C in January, annual precipitation was 2720 mm, and maximum snow accumulation was 12 cm in January (data from the Japan Meteorological Agency between 1971 and 2000). Annual precipitation in the Kujyu mountain area is reported to be up to 3500 mm [28]. The upper part (southern area) of the Tadewara mire is covered with a grassland dominated by *Miscanthus sinensis* Anderss. and the lower part (northern area) of the mire is covered by mesotrophic to ombrotrophic mire vegetation dominated by *Phragmites australis* (Cav.) Trin. ex Steud., *Moliniopsis japonica* (Hack.) Hayata, and *Hydrangea paniculata* Sieb. et Zucc. Two *Sphagnum* species, *Sphagnum palustre* L. (section Palustria or Sphagnum) and *Sphagnum fimbriatum* Wils. ex Wils. & Hookf. (section Acutifolia) distribute in the central area of the mire community. The depth of the peat layer at the center of the *Sphagnum* dominated mire was 4.2 m and the layer lower than 163 cm contains large amounts of volcanic mineral deposition (C contents < 5% w/w; Haraguchi *et al.*, unpublished data).

Another sampling site, the East Ochiishi mire was in the Ochiishi district, Nemuro, in north-eastern Japan. Some ombrogenous mires were established on the coastal terrace at 40 - 50 m a.s.l, having been formed by the Nemuro Group in the Upper Cretaceous. The annual mean temperature in the East Ochiishi mire was 5.7˚C, average daily maximum temperature was 20.5˚C in August, average daily minimum temperature was –9.3˚C in February, annual precipitation was 1031 mm, and maximum snow accumulation was 23 cm in February (data from the Japan Meteorological Agency between 1971 and 2000). A *Picea glehnii* (Fr. Schm.) Masters. forest was estab- lished on the mire in conjunction with the *Sphagnum*- dominated mire [29]. The site description and description of the vegetation structure of the mires in the Ochiishi district appear in [29]. *Sphagnum* plants were collected from the East Ochiishi mire, which has a peat accumula- tion of 1.3 - 1.5 m. Several tephra layers are included in the peat layer, and the latest layer of the Holocene tephra originating from Tarumae Volcano (Ta-a; 1739 AD) ap- pears at a depth of 10 - 15 cm. The dominant *Sphagnum* species in the mire are *Sphagnum fuscum* (Schimp.) Klinggr. (section Acutifolia) and *S. papillosum* Lindb. (section Palustria). *Sphagnum fallax* Klinggr. (section Cuspidata), *S. girgensohnii* Russ. (section Acutifolia) and *S. squarrosum* Crome (section Squarrosa) were abundant on the *P. glehnii* forest floor. We collected *S. papillosum*, *S. fuscum* and *S. fallax* from the East Ochiishi mire.

Sphagnum samples of 10 cm length with capitula were excised in the field and stored in air-tight plastic bags immediately after sample collection. Samples were trans-

ferred to the laboratory at room temperature and samples were cultivated at T = 25˚C under 12L12D illuminated with PPFD is 40 $\mu mol \cdot m^{-2} \cdot s^{-1}$ until photosynthesis measurements were made. Plants were submerged in pure water except for the capitula and water was supplied at 1 - 2 day intervals, thus preventing plants from entering the atmosphere. Photosynthesis measurements were made within 10 days from the beginning of cultivation and the plant samples were kept in good physiological condition for the measurement.

2.2. Measurements of Photosynthesis and Dark Respiration Rates

Capitula segments of 1 cm from the apex were excised from the shoots of *Sphagnum* plants and regularly arranged on Petri dishes. Twelve capitula were used for measurements for *S. palustre*, *S. fimbriatum*, *S. papillosum* and *S. fallax*, whereas 15 capitula were used for *S. fuscum*. Plant materials were submerged in water and preliminary illumination was provided in the growth chamber at T = 20˚C for more than 24 hours at PPFD = 90 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Water in the Petri dish was removed just before the photosynthesis measurements.

Photosynthetic rates and dark respiration rates for the *Sphagnum* spp. were measured by CO_2 exchange rate in a chamber with a constant flow of air. Ambient air (CO_2 concentration 420 - 470 ppm) was pooled in a gas bag (3.5 m^3) and supplied the air at 1.0 L·min^{-1} to the chamber after saturation of humidity by flushing through water. Concentration of CO_2 before and after the chamber was measured by infrared CO_2 analyzer (LI-COR, LI-840). The chamber (13 cm × 10 cm × 4.5 cm) was made of polypropylene and the upper surface of the chamber was made of acryl transparency plate (10.2 cm × 7 cm). The chamber was placed in a 100 L water bath and water temperature was controlled by a temperature control system (TAITEC, CL-150R). Irradiation was provided by four 500 W halogen lamps and the photon flux density of photosynthetically active radiation (PPFD) was measured by a PPFD sensor in water (LI-COR, LI- 250A).

Petri dishes with *Sphagnum* capitula were placed in the plastic chamber. The chamber was submerged in water and water temperature was controlled by circulating water. Measurement of CO_2 concentration started 30 min after setting up the chamber. Readings of the CO_2 concentration became stable within 30 min. Concentrations of CO_2 were recorded at 1 sec intervals. CO_2 concentrations flowing both in and out of the chamber were alternately measured at 10 sec intervals. PPFD at the surface of plant samples and water temperature just at the surface of the chamber were recorded for each measurement.

PPFD changed from ca. 800 $\mu mol \cdot m^{-2} \cdot s^{-1}$ to 0

$\mu mol \cdot m^{-2} \cdot s^{-1}$ and CO_2 concentrations were measured at 15 different PPFD levels. Dark respiration was measured by covering the chamber with a dark net. Temperature was changed from 5°C to 40°C at 5°C intervals. A chamber without plant samples was used as a reference and the CO_2 concentration of the reference chamber was used as a blank.

After measurement of the CO_2 exchange rate, plant samples were dried at T = 70°C for 24 hours and dry weights of the plants were measured. Photosynthetic and respiration rates were calculated on a dry-weight basis.

3. Results

Absolute photosynthetic rates of *Sphagnum* spp. showed high variance between individual plants, and we presented PPFD-photosynthetic rate response curves by the relative rate (%) per maximum rate within the measurements using the same plant samples (**Figure 1**). Absolute values for photosynthetic rate appear in **Figure 2**. PPFD-gross photosynthetic rate response curves showed significant temperature dependence for every species. *S. fimbriatum* from the Tadewara mire showed the maximum photosynthetic rate at T = 25°C, and the rate maintained higher values within the temperature range of T = 15°C - 35°C (**Figure 1(a)**). Within the temperature range of 15°C to 35°C, the maximum photosynthetic rate was obtained at PPFD = 320 - 450 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and the rate decreased at PPFD > 450 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The gross photosynthetic rate of *S. fimbriatum* showed lower values at T = 5°C, 10°C and 40°C, and the maximum photosynthetic rates were obtained at PPFD = 200 - 250 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at T = 5°C and 10°C.

S. palustre from the Tadewara mire showed maximum photosynthetic rates at T = 25°C - 30°C and the rates remained almost the same within the temperature range (**Figure 1(b)**). At T = 35°C, photosynthetic rates for *S. palustre* significantly decreased at PPFD > 490 $\mu mol \cdot m^{-2} \cdot s^{-1}$, whereas the decrease in photosynthetic rates at PPFD > 660 $\mu mol \cdot m^{-2} \cdot s^{-1}$ was not significant at T = 25°C and 30°C. Photosynthetic rates for *S. palustre* at T = 5°C were the lowest, and the rate decreased at PPFD > 120 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The gross photosynthetic rate decreased at PPFD > 80 $\mu mol \cdot m^{-2} \cdot s^{-1}$ at T = 40°C.

S. fuscum from the East Ochiishi mire showed maximum gross photosynthetic rate at T = 35°C and the higher rate was maintained within the temperature range of T = 30°C - 40°C (**Figure 1(c)**). At T = 30°C, the gross photosynthetic rate of *S. fuscum* slightly decreased at PPFD > 550 $\mu mol \cdot m^{-2} \cdot s^{-1}$, whereas no decrease in photosynthetic rate at high light intensity was observed at T = 35°C and 40°C. The photosynthetic rate for *S. fuscum* at T = 5°C was the lowest.

S. papillosum from the East Ochiishi mire showed a maximum photosynthetic rate at T = 35°C, and the rate maintained higher values within the temperature range of T = 30°C - 35°C (**Figure 1(d)**). Even at T = 40°C, the photosynthetic rate of *S. papillosum* remained almost the same as that measured at T = 25°C. The photosynthetic rate of *S. papillosum* showed its lowest value at T = 5°C, and the rate decreased at PPFD > 530 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

S. fallax from the East Ochiishi mire showed a maximum photosynthetic rate at T = 30°C, and the rate maintained higher values within a temperature range of T = 25°C - 40°C (**Figure 1(e)**). The photosynthetic rate of *S. fallax* showed its lowest value at T = 5°C, and the rate decreased at PPFD > 270 $\mu mol \cdot m^{-2} \cdot s^{-1}$.

Light intensity at the saturated photosynthetic rate was 200 - 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (**Figure 1**) and the value was quite similar to the reported values [30-32]. Many of the response curves showed a decrease in photosynthetic rate when PPFD exceeded 300 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Thus, neither the hyperbolic response curve nor the non-rectangular hyperbola model [33] was applicable for the regression of the PPFD-photosynthesis response curve obtained here. At first we applied the non-rectangular hyperbola model excluding the experimental data for higher PPFDs than that at which the maximum photosynthetic rate was obtained. The non-rectangular hyperbola model is represented by the formula:

$$\theta P_s^2 - \left(P_{max} + \alpha I - \theta R_d \right) P_s$$
$$+ \alpha I \left(P_{max} - \left(1 - \theta \right) R_d \right) - R_d P_s = 0$$

where P_s is the net CO_2 assimilation rate ($\mu mol \cdot CO_2 \cdot m^{-2} \cdot s^{-1}$), I is the PPFD ($\mu mol$-photon$\cdot m^{-2} \cdot s^{-1}$), R_d is the rate of dark respiration expressed as CO_2 production (μmol-$CO_2 \cdot m^{-2} \cdot s^{-1}$), P_{max} is the light-saturated rate of gross CO_2 assimilation (μmol-$CO_2 \cdot m^{-2} \cdot s^{-1}$), and θ and α are constants determining curvature at the shoulder and apparent quantum efficiency (initial slope at zero irradiance of the light-photosynthetic rate relationship curve), respectively. R_d was obtained from the experimental data, and the light response curve of the gross photosynthetic rate was obtained by substituting $R_d = 0$ in the equation.

Maximum photosynthetic rates (P_{max}) estimated by the non-rectangular hyperbola model (excluding data for higher PPFDs if the PPFD-photosynthesis curves showed a decreasing tendency at higher PPFDs) were obtained at T = 35°C for *S. palustre*, *S. fuscum* and *S. papillosum*, and at T = 30°C for *S. fimbriatum* and *S. fallax* (**Figure 2(a)**). Although temperature dependence for P_{max} was significant (p < 0.05) only for *S. palustre* by the Kruskal-Wallis test, P_{max} at T = 40°C was 70% - 85 % of P_{max} at T = 35°C for northern species (*S. fuscum*, *S. fallax* and *S.*
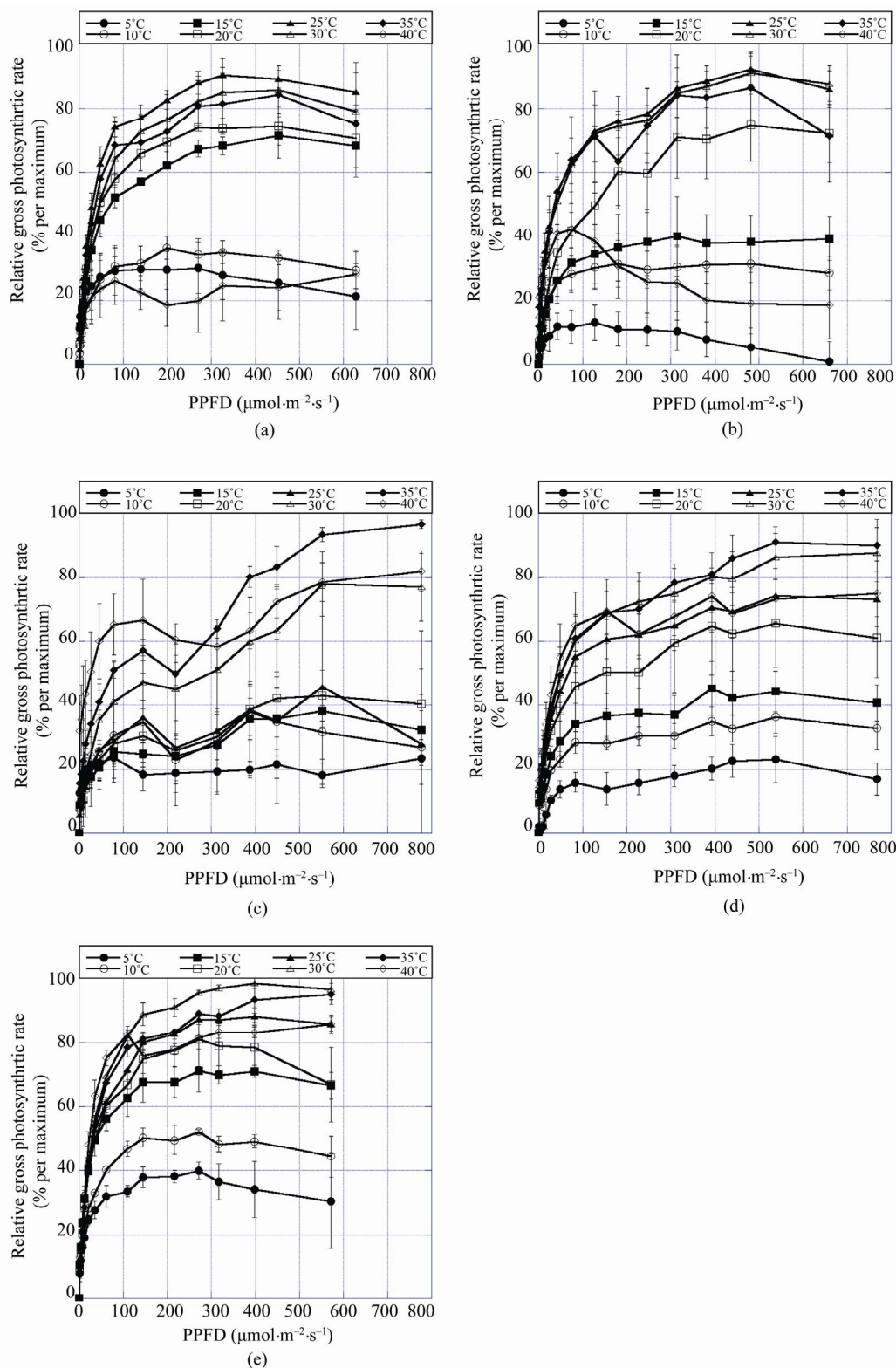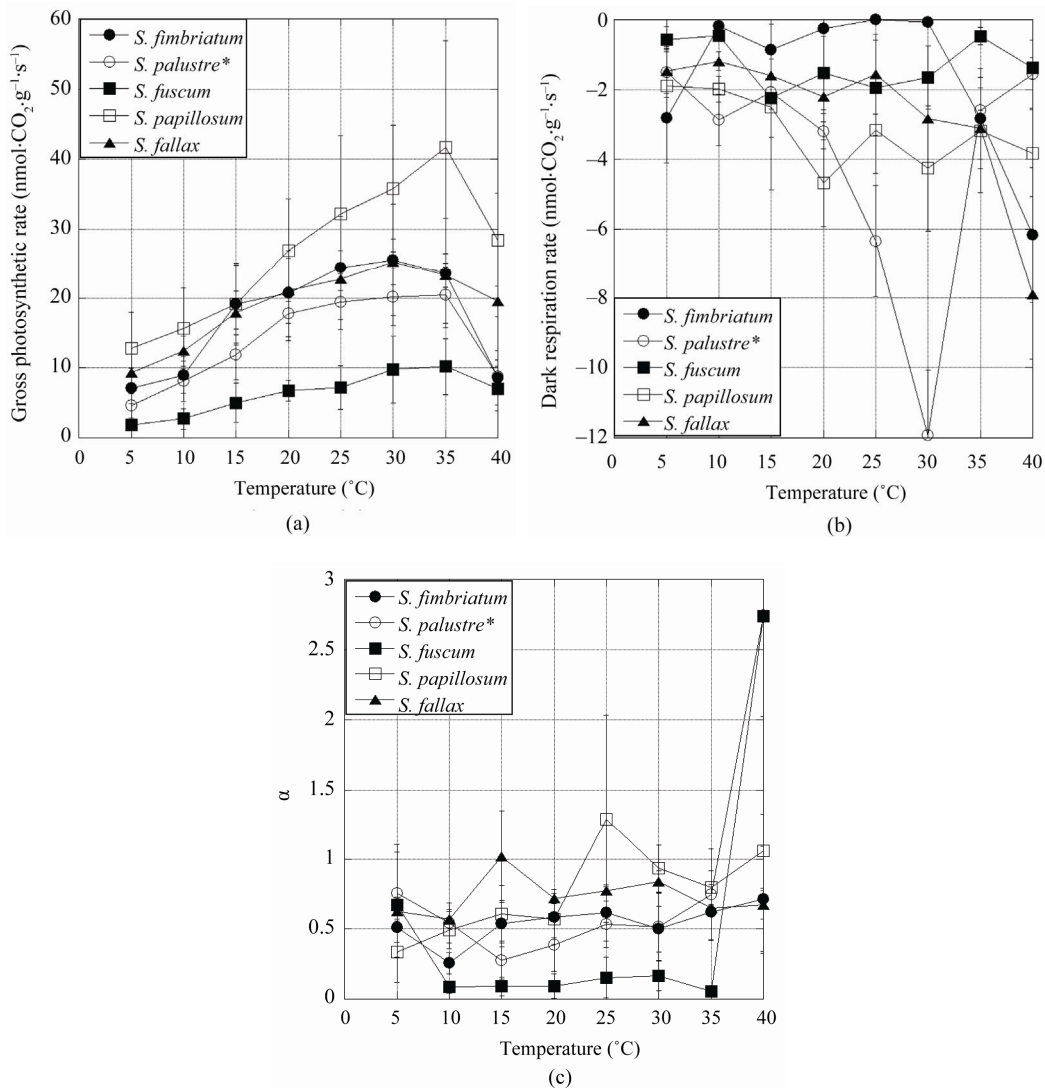
AJPS

Figure 1. Relative gross photosynthetic rate (% per maximum) and PPFD relationship curve of (a) *Sphagnum fimbriatum***; (b)** *S. palustre* **(from the Tadewara mire in northern Kyushu, Japan); (c)** *S. fuscum***; (d)** *S. papillosum***; (e)** *S. fallax* **(from the East Ochiishi mire in north-eastern Hokkaido, Japan) at temperatures of 5˚C, 10˚C, 15˚C, 20˚C, 25˚C, 30˚C, 35˚C, and 40˚C.**

Temperature Dependency of Photosynthesis of *Sphagnum* spp. Distributed in the Warm-Temperate and the
Cool-Temperate Mires of Japan

721

Figure 2. (a) Temperature dependence of gross photosynthetic rate (P_{max}), (b) dark respiration (R_d) and (c) apparent quantum efficiency (slope of PPFD-photosynthesis response curve at 0 irradiation; (α) of *Sphagnum fimbriatum* (●), *S. palustre* (○), *S. fuscum* (■), *S. papillosum* (□), and *S. fallax* (▲). P_{max} and α were estimated using a non-rectangular hyperbola model excluding data for higher irradiation if PPFD-photosynthetic rate curves showed decreasing tendencies at higher irradiation. R_d was measured directly.

papillosum), whereas the ratio was 30% - 40% for southern species (*S. fimbriatum* and *S. palustre*). Relative gross P_{max} (% per maximum) determined by using the data for relative photosynthetic rate within the same plant samples presented in **Figure 1** showed significant temperature dependence for every species: *S. fimbriatum* (p < 0.01), *S. palustre* (p < 0.01), *S. fuscum* (p < 0.01), *S. papillosum* (p < 0.01) and *S. fallax* (p < 0.05) by the Kruskal-Wallis test.

Dark respiration (R_d) for *S. fimbriatum* increased over T = 30°C and showed a maximum at T = 40°C (**Figure 2(b)**). *S. fallax* showed a tendency similar to that of *S.*

fimbriatum and R_d increased over T = 30°C and showed a maximum at T = 40°C. R_d for *S. fuscum* and *S. papillosum* showed a maximum around T = 15°C - 20°C, although the temperature dependence was not significant. *S. palustre* showed a maximum R_d at T = 30°C, but the extremely high R_d value for *S. palustre* could be due to some error in measurement. Temperature dependence for R_d was significant (p < 0.05) only for *S. palustre*.

Apparent quantum efficiency (α) did not show significant temperature dependence (p > 0.05) for any of the species (**Figure 2(c)**). However, *S. palustre* and *S. fuscum* showed extremely high values at T = 40°C. Slope of

the PPFD-photosynthetic rate response curve at zero irradiance determined by using the relative photosynthetic rate (% per maximum) that corresponds to α also showed no significant temperature dependence ($p > 0.05$) for any of the species.

After the estimation of photosynthetic parameters using the non-rectangular hyperbola model, a fourth function equation was applied for the experimental data, including all the data at higher PPFDs. The equation provided the best fit for most of the PPFD-photosynthesis response curves which showed a decline of photosynthetic rate at higher PPFDs. Then we used the fourth function equation to obtain an estimated value. However, this equation does not have any physiological meaning for describing the regression of photosynthetic rates in relation to PPFDs.

Photosynthetic rates for the five *Sphagnum* species distributed in the Tadewara mire and the East Ochiishi mire showed obvious temperature dependence (**Figure 3**). Fits for the photosynthesis response curves in relation to PPFD were found using the fourth function equation and were used to estimate the rates at low light intensity (PPFD = 150 μmol·m^{-2}·s^{-1}) and high light intensity (PPFD = 500 μmol·m^{-2}·s^{-1}). *S. fimbriatum*, *S. palustre* and *S. fuscum* showed significant differences in photosynthetic rates among various temperature conditions by the Kruskal-Wallis test, both at the low and high light intensities ($p < 0.05$ for *S. palustre* at PPFD = 150 μmol·m^{-2}·s^{-1}, $p < 0.001$ for *S. fuscum* at PPFD = 500 μmol·m^{-2}·s^{-1}, $p < 0.01$ for others). *S. fallax* showed significant differences in photosynthetic rates among various temperature conditions at PPFD = 500 μmol·m^{-2}·s^{-1} ($p <$

0.05; **Figure 4**). *S. papillosum* did not show significant dependence between its photosynthetic rate and the varying temperature conditions ($p > 0.05$).

Although temperature dependence at optimal PPFDs that showed maximum rates for gross photosynthesis at each temperature was significant only for *S. palustre* ($p < 0.05$), PPFD at P_{max} tended to increase with increasing temperature. *S. palustre* showed the lowest value at T = 40°C.

4. Discussion

The temperature dependence of photosynthetic rate was observed for every species of *Sphagnum* studied here. Apparent quantum efficiency (α) did not show significant temperature dependence (**Figure 2(c)**), and hence biochemical reaction is the rate-determining reaction depending on temperature. Temperature dependence levels in relation to the photosynthetic rate were quite similar for all the species at a temperature of T < 25°C, and the Q_{10} value from T = 10°C to 20°C was 1.70 - 2.47 (**Figure 2(a)**).

Temperature dependence of the photosynthetic rates at high temperature (T > 25°C) showed differences among the species. *S. fimbriatum* and *S. palustre* from the Tadewara mire showed significant decreases of photosynthetic rate at T = 40°C compared to the results for T = 35°C and the rates of *S. fimbriatum* and *S. palustre* at T = 40°C were 36% and 43% of those at T = 35°C, respectively, whereas the rates at T = 40°C for *S. fuscum*, *S. papillosum* and *S. fallax* from the East Ochiishi mire were slightly lower than the rates at T = 35°C. The rates for *S. fuscum*, *S. papillosum*, and *S. fallax* at T = 40°C
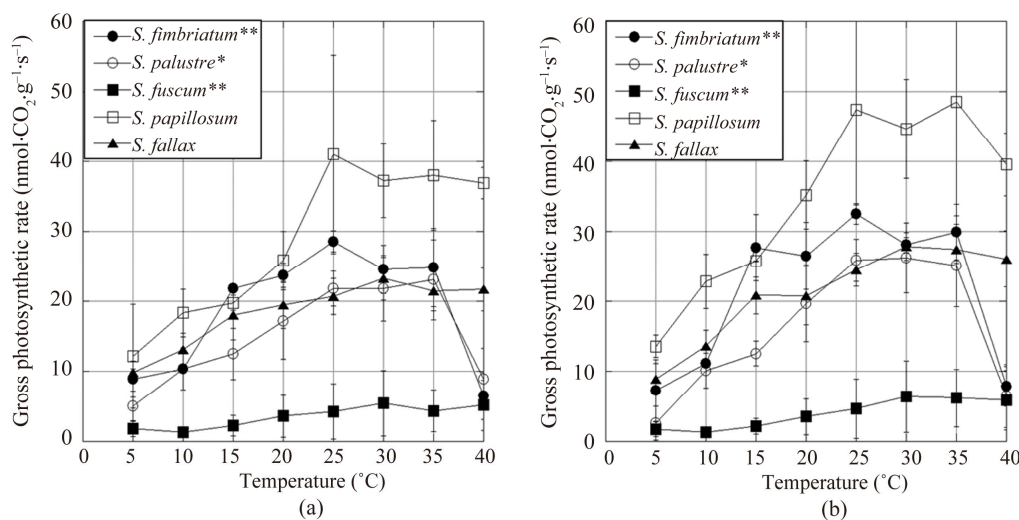
Figure 3. Temperature dependence of gross photosynthetic rate (P_{max}) of *Sphagnum fimbriatum* (●), *S. palustre* (○), *S. fuscum* (■), *S. papillosum* (□), and *S. fallax* (▲) at (a) PPFD = 150 μmol·m^{-2}·s^{-1} and (b) PPFD = 500 μmol·m^{-2}·s^{-1} estimated based on regression using a fourth function equation.
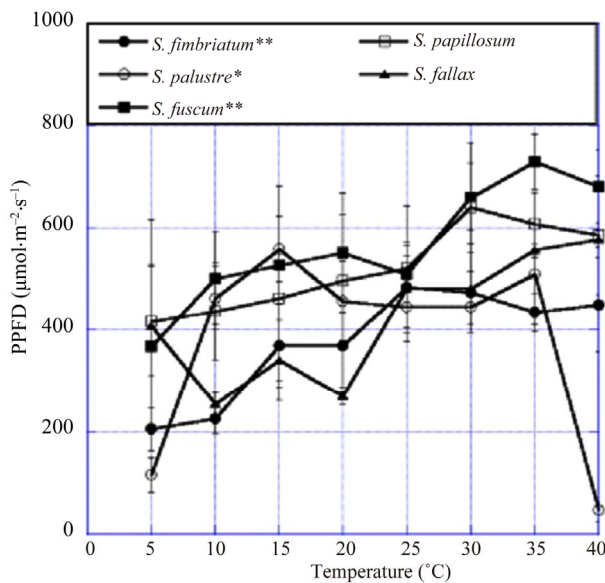
Figure 4. Optimal PPFDs showing maximum rates of photosynthesis in PPFD-gross photosynthesis response curves measured at each temperature. Species are *Sphagnum fimbriatum* (●), *S. palustre* (○), *S. fuscum* (■), *S. papillosum* (□), and *S. fallax* (▲).

were 69%, 68% and 84% of those obtained at T = 35°C, respectively.

Thus we found that the photosynthetic rates of the two species from the Tadewara mire decreased when temperature exceeded 35°C, whereas the rates of the three species from the East Ochiishi mire did not decrease when the temperature was 40°C.

Especially under low temperature conditions, the photosynthetic rates for *Sphagnum* spp. under conditions of high PPFD were lower than rates obtained under low PPFD conditions. This shows that photosynthesis was inhibited by high PPFD in low temperature environments. Inhibition of photosynthesis by high PPFD levels has been reported for some species, e.g., tomato, *Nicotiana tabacum*, and *Camellia sinensis* at T = 0°C - 15°C [34-37]. Most of these reports are for vascular plants sensitive to low temperature stress. Our observations showed that inhibition of photosynthesis by high PPFDs under low temperature conditions was evident for *Sphagnum* spp. whose distribution was mostly in the circumpolar region.

Apparent quantum efficiencies (α) were not significantly different among the various temperature conditions created for each of the species. This implies that photoreaction in *Sphagnum* plants is not significantly affected by temperature.

Dark respiration (R_d) commonly shows a tendency to increase with increasing temperature, and the net photosynthetic rate and the consequent net primary production

showed maximum levels at temperatures lower than the optimum temperature for gross photosynthetic rate. However, R_d in our measurements of *Sphagnum* spp. did not significantly increase up to T = 40°C. Respiration in *Sphagnum* plants showed an adaptive trend as photosynthetic capacity at higher temperatures.

Although *Sphagnum* species dominate in mires in low temperature regions and these species are the successful plants in low temperature environments, the physiological properties of *Sphagnum* may not have fully adapted to low temperature conditions. Considering the fact that *Sphagnum* spp. distribute also in tropical lowland areas with high temperatures [38], *Sphagnum* species may have potential for distribution in tropical regions.

5. Acknowledgements

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