# GROWTH AND PRODUCTION OF *SPHAGNUM* MOSSES FROM TAKADAYACHI MOOR IN HAKKODA MOUNTAINS, NORTHEAST JAPAN 1. —DRY MATTER PRODUCTION ESTIMATED FROM PHOTOSYNTHESIS AND RESPIRATION—*

SATOSHI FUKUSHIMA**, ATSUSHI KUME**, YOSHIO INO**
and YUKIRA MOCHIDA***

## INTRODUCTION

When studies about the ecophysiological function in moor ecosystems or the conservation of it are planned, it is a fundamental matter to get hold of the growth or matter production of *Sphagnum* mosses which usually dominate the ecosystems. Ecophysiological studies of *Sphagnum* have been done in the northern regions of Europe and America (e.g. Clymo, 1970; Clymo, 1973; Clymo and Heyward, 1982; Grigal, 1984; Moor, 1989; Pakarinen, 1978; Rydin and McDonald, 1985; Titus and Wargner, 1984; Wieder and Lang, 1983). In Japan, ecophysiological studies about *Sphagnum* were few. There have been a few studies about the production or growth of *Spagnum*, in Ozegahara Moor (Kashimura and Tachibana, 1982), in Akaiyachi moor (Kashimura and Kantani, 1987) and in Furen mire (Tachibana *et al.*, 1987).

The dry matter production or the growth of *Sphagnum* has been estimated with the elongation rate and the density in the habitat (Kashimura and Kantani, 1987; Kashimura and Tachibana, 1982; Moor, 1989; Rochehort *et al.*, 1990; Wallen *et al.*, 1988; Wieder and Lang, 1983). The measurement of the elongation have been carried out with innate markers, nets, cranked wires, etc. But every method seems to have some wrong effects on mosses. For example, Russell (1984) reported that the growth of mosses was inhibited by their contact to metal equipment, such as nets and cranked wires. And also, Clymo (1970) reported that growth in length was not closely correlated with growth in weight unless reffered to a paticular environment.

An indirect method, like photosynthesis, is applied to the measurement of the

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* Contribution from the Mt. Hakkoda Botanical Laboratory, No. 153
** Department of Biology, School of Education, Waseda University, Shinjukuku, Tokyo 169-50, Japan
*** The Mt. Hakkoda Botanical Laboratory, Tohoku University, Aobaku, Sendai 980-77, Japan

growth or the matter production. But the photosynthetic rate of *Sphagnum* is controlled by environmental factors, i.e., temperature, radiation (Harley *et al.*, 1989), water content (Dilks and Procter, 1979 ; Ino and Takamine, 1994 ; Murray *et al.*, 1989 ; Titus *et al.*, 1983) etc. and also, by internal factors, i.e., photosynthetic activity, seasonal growth pattern, etc. The changes of temperature and radiation are measured easily but, the continuous measurement of the water content is difficult. As a matter of fact, the production studies with water content have been few.

In this study, photosynthesis of 3 species of *Sphagnum* mosses sampled in a moor on the slope of Hakkoda Mts. were measured monthly in the laboratory during a growing season. Photon flux density and moss temperature were measured in their habitats during four growing seasons, from May to October. Net production rate of each moss population under the optimum water content was calculated with these data. Then, the calculated production rates were corrected with the estimated daily water contents of mosses in the habitats and the respiration amounts in the nonphotosynthetic tissues were taken away from the corrected production rates.

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## MATERIALS AND METHODS

1. Sampling site

Materials were sampled in Takadayachi moor (40°37′N, 140°53′E, 1,000 m alt., ca. 5.9 ha) which was situated on the south-east slope of Mt. Hakkoda-Ohdake in Aomori Prefecture (Fig. 1). *Sasa kurilensis* surrounded the moor and the outside was covered with evergreen conifer, *Pinus pumila* and *Abies mariesii*. In this moor, some species of *Sphagnum* existed with *Drosera rotundifolia*, *Andromeda polifolia* and *Vaccinium oxycoccus*. *Moliniopsis japonics* and *Sanguisorbs tenuifolia* were dominated in summer. *Sphagnum nemoreum* and *S. papillosum* grew in hummock parts and *S. tenellum* was in hollow parts. Yoshioka (1963) described in detail the vegetation of Takadayachi moor.

2. Sampling methods

Samples of 3 species of dominant *Sphagnum* were taken monthly from May to October in 1989. Two blocks, about 12 cm × 12 cm and 10 cm depth, per a species were cut from each population and each block was put into a polyethylene bag. These samples were put in an ice box and were transported to Waseda University at Tokyo within two days. In laboratory, the samples were held in a growth box at 10°C, 100 $\mu$mol $m^{-2}$ $s^{-1}$ PFD (Photon flux density) and 12L-12D until the measurement of photosynthesis.

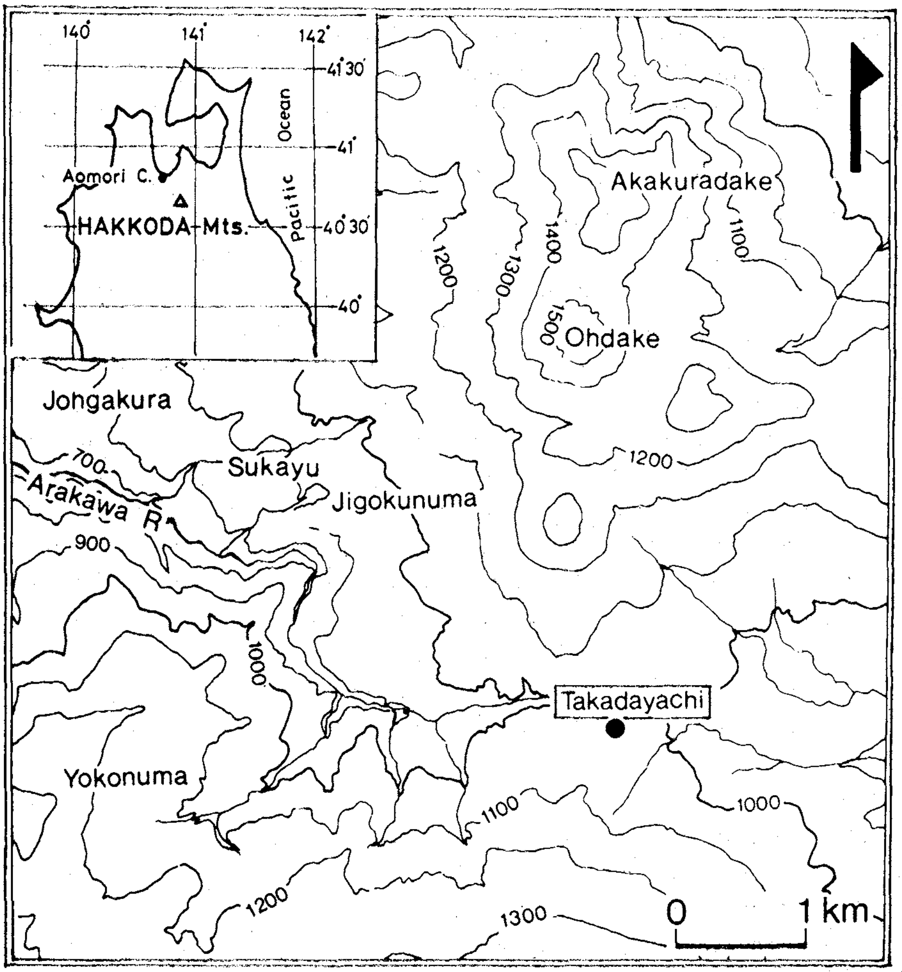



Fig. 1. The location investigated in the northern Hakkada Mountains.

3. Measurement of photosynthesis

Two infrared $CO_2$ gas analyzers (VIA-300, Horiba Ltd, Kyoto), an assimilation chamber with a temperature controller (MC-A3W, Koito Industries Ltd., Yokohama) and 400 W metalhalide lamp (BOC400C-U, Mitsubishi Electric Co. Ltd., Yokohama) were used for the measurement of photosynthesis. At the day before the measurement of photosynthesis, the green layer, about 2 cm in thickness, of moss block was cut out and the layer was put in a 9 cm shallow Petri dish in the natural growing density. First experiment was done to find out the optimum water content for net photosynthesis. Fully moistened sample was put into the assimilation chamber and the $CO_2$ exchange was measured at 15°C, 1,100 $\mu$mol $m^{-2}$ $s^{-1}$ PFD and 350-370 ppm $CO_2$. The Petri dish with the sample was taken out from the assimilation chamber every 20 or 30 min and after being weighed, it was returned to the chamber. This treatment was repeated after the $CO_2$ uptake began to drop. It was supposed that the water content just before the photosynthetic rate began to drop was the optimum water content for net photosynthesis.

The photosynthetic rate of each species was measured at 4 different levels of moss temperature, i.e., 25, 20, 15 and 10°C, and 5 levels of PFD, i.e., 1,100, 700, 300, 120 and 0 $\mu$mol $m^{-2}$ $s^{-1}$ with double samples at the optimum water content. After that, the sample was dried at 80°C for the measurent of the dry weight.

4. Measurement of respiration in nonphotosynthetic layer

The upper part of the brown colored portion lives under the photosynthetic layer. It is thought that the substance for the respiration of brown portion is translocated from photosynthetic layer, because matter production is not carried out in the brown layer. Respiration of the upper brown layers, 2-4 cm and 4-6 cm from the top was measured for each species. In *S. tenellum*, the tissue deeper than 4 cm, and in other species, the tissue deeper than 6 cm were decomposing.

The samples were cut out from the blocks and put into shallow Petri dish in the natural density. The respiration was measured with the same equipment as the measurement of photosynthesis without irradiance. The temperature was 5, 10, 15, 20 and 25°C. The water content was not controlled, because it was clear that respiration rate was not affected by the water content in the natural growing condition.

5. Measurement of microclimate

The microclimate, i.e., air temperature, moss temperature and PFD, at Takadayachi moor were measured for the calculation of matter production. The moss temperature of each species was measured at 1 cm below the surface with a thermistor sensor for 10 s per every 30 min and these data were stored with a logger (KADEC-U, KONA SYSTEM, Sapporo). Photon flux density was measured at about 30 cm above the surface with a sensor (IKS-25, Koito Industries Ltd., Yokohama) which was turned right above, every 10 min. The data were stored with a logger (KADEC-UP, KONA SYSTEM). The measurement was carried out from May to October, from 1990 to 1993. The temperature data in *S. papillosum* habitat in 1990, and PFD from May to July in 1992 were not recorded because of the trouble of the loggers.

6. Calculation of net production

A non-linear multiple regression model given by Kappen *et al.* (1988) was used in this study:

$$\mathbf{Pn} = p_1 + p_2 * \mathbf{T} + p_3 * \mathbf{T}^2 + p_4 * \ln(\mathbf{I}+\mathbf{1}) + p_5 * (\ln(\mathbf{I}+\mathbf{1}))^2 + p_6 * \mathbf{T} * \ln(\mathbf{I}+\mathbf{1}) \quad (1)$$

where **Pn**, **T** and **I** is net photosynthetic rate, the moss temperature and PFD, respectively. The $P_n$ in this equation is the parameter of each component. The parameters in each month, from May to October, were decided with the relationships between photosynthetic rates, and PFD and the moss temperature measured monthly in 1989. The correlation coefficiencies of the equations were in the ranges from 0.99 to 0.72.

Hourly net photosynthetic rates were calculated by PFD and the moss temperature in the habitats. The relationship between the respiration rate and the moss temperature was shown with an equation:

$$\mathbf{R} = q_1 + q_2 * \mathbf{T} + q_3 * \mathbf{T}^2$$

where **R** and **T** is the respiration rate and the moss temperature, respectively and $q_n$ is the parameter of each component.

The parameter $q_n$ of each month equation was decided with the respiration rate and the moss temperature. The correlation efficiencies of monthly equations were in the range from 0.99 to 0.88.

The hourly respiration rate was calculated with hourly mean moss temperature. Daily net production was calculated with the hourly photosynthetic rates, hourly respiration rates and mean carbon content, 44%, of mosses.

7. Water content in habitat

The daily changes of the water content in photosynthetic tissue of each species were measured in the habitat from 16 to 22, September, 1993 and for a few days in August, 1991. In order to measure the water content, ten shoots were sampled, two or three times a day, and the samples were put into polyethylene bags. These bang were put in an ice box and transported to the laboratory. After the fresh weight was measured, each sample was dried at 80°C in an oven for over 48 h and the dry weight was measured. The water content was showed as percentage of water amount to the dry weight.

## RESULTS

1. Climate

Daily cumulative PFD (DPFD) is shown in Fig. 2 as the daily mean of every 10 days. The highest DPFD was recorded in May or July and was over 40 mol $m^{-2}$ $day^{-1}$. The highest PFD in a day was over 2,000 $\mu$mol $m^{-2}$ $s^{-1}$. The DPFD decreased after July and in October it dropped to 20 mol $m^{-2}$ $day^{-1}$. Daily mean moss temperature is shown in Fig. 3 as the mean of every 10 days. In 1990, the temperature of two species except *S. papillosum* is shown, and in 1993, the air temperature is added. The daily mean moss temperature was highest in late July and early August and it was over 20°C. The daily maximum temperature of each species was often over 30°C in summer. The temperature of *S. papillosum* was higher than the other species in the summer of 1991 but this tendency was not recognized in 1992 and 1993. After August, the moss temperature dropped and in

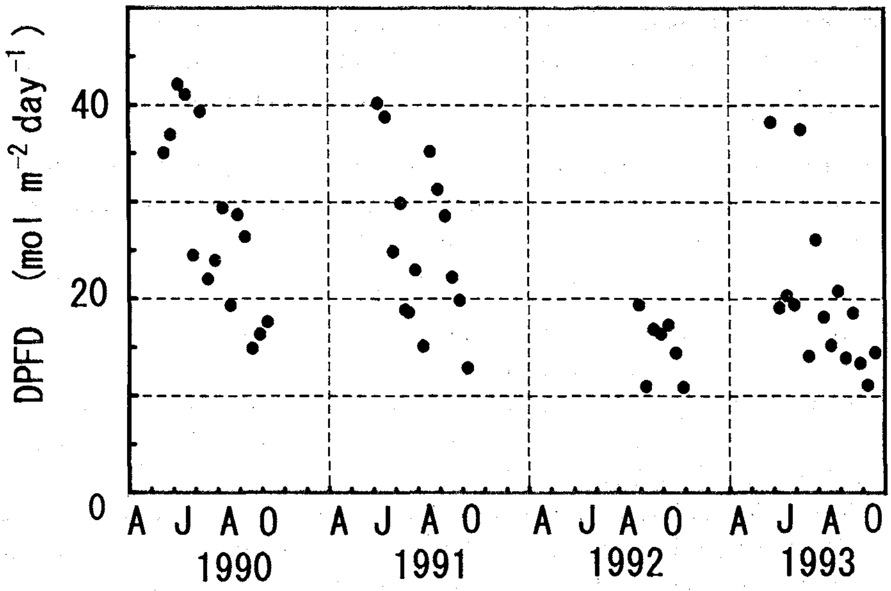



Fig. 2. Seasonal changes of daily cummurative photon flux density (DPFD) at Takadayachi moor. Each point shows the mean density of tenor eleven days.

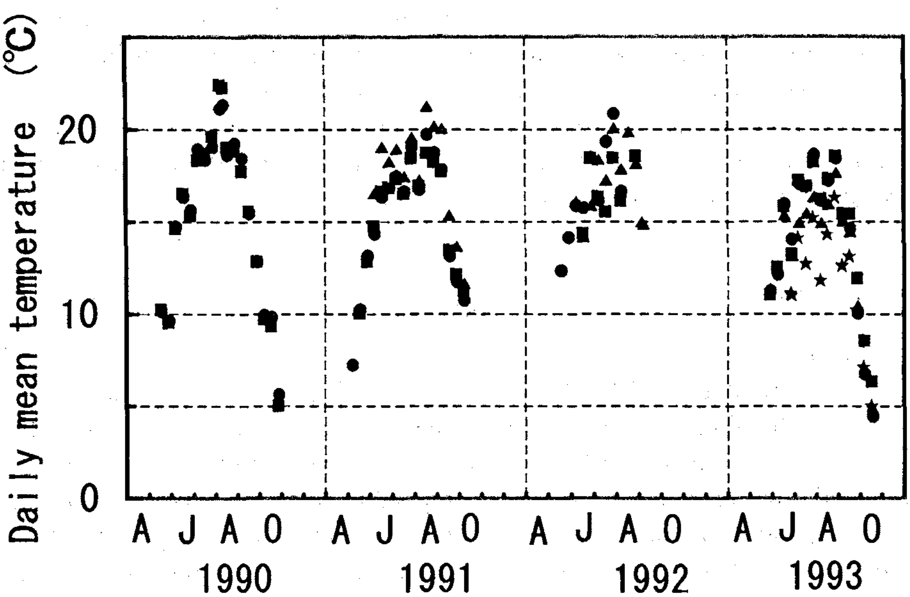
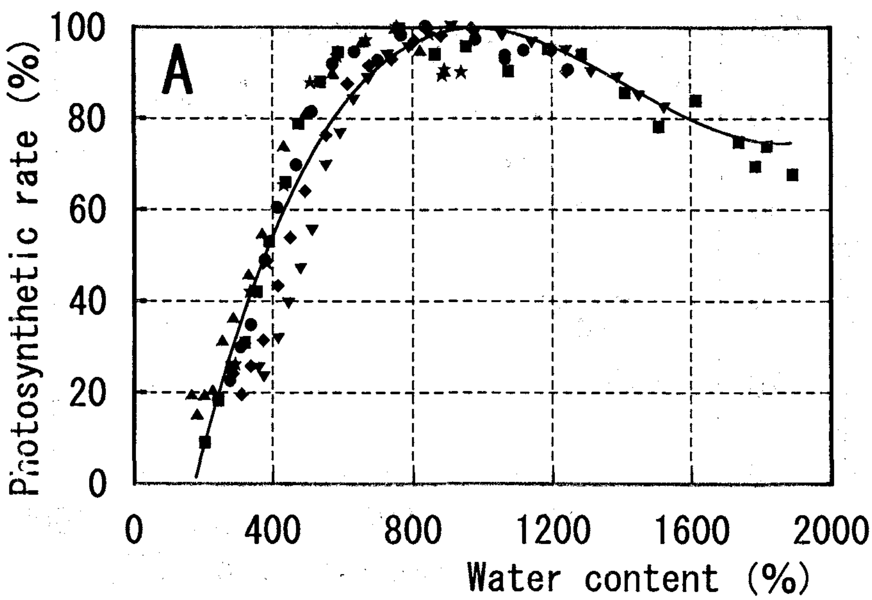
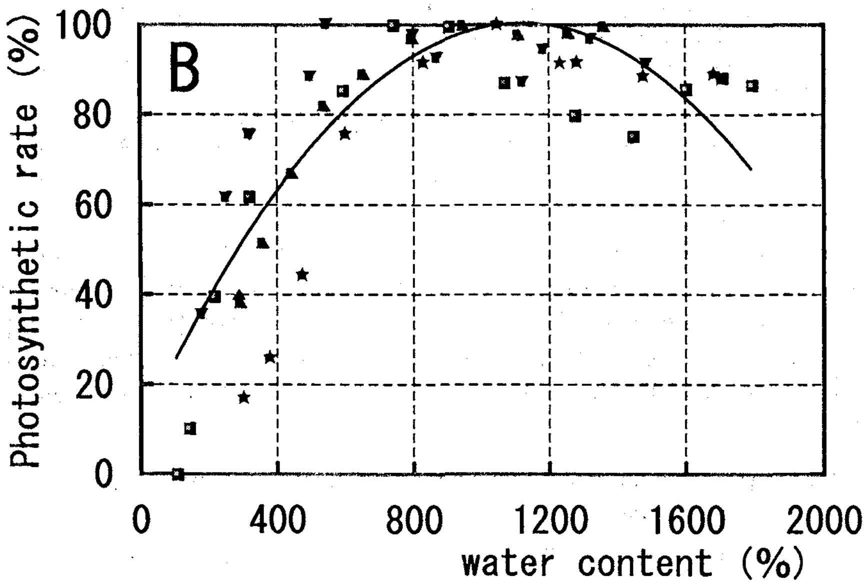



Fig. 3. Seasonal changes of daily mean moss temperature of *Sphagnum tenellum*, *S. papillosum* and *S. nemoreum* and the air temperature at Takadayashi moor. Each point shows the mean temperature of ten or eleven days. The air temperature was measured only in 1993. The moss temperature of *S. papillosum* in 1990 was not measured because of the trouble of the equipment.
■ : *S. tenellum*, ▲ : *S. papillosum*, ● : *S. nemoreum*, ★ : air temperature




late October, it was below 5°C. The daily mean air temperature was lower than the moss temperatur.

2. Relationships between net photosynthetic rates and water contents

The relationships were taken 4 to 6 times from July to October in 1989. Monthly samples of each species had different maximum net photosynthetic rates but the optimum water contents were equal. The optimum content of each

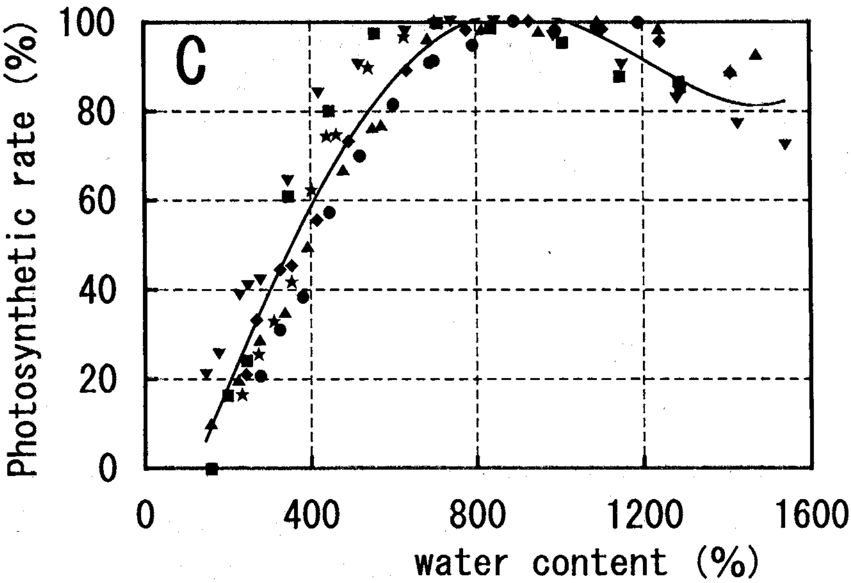



Fig. 4. The relationship between the water content of mosses and the relative photosynthetic rates to the maximum rates.
A : *S. tenellum*, ■ : Jul. 7 ; ◆ : Aug. 3 ; ▲ : Aug. 5 ; ★ : Aug. 30 ; ● : Sep. 23 ; ▼ : Oct. 26.
B : *S. papillosum*, ■ : Jul. 5 ; ★ : Aug. 29 ; ● : Sep. 23 ; ▼Oct. 25
C : *S. nemoreum*. ■ : Jul. 5 ; ◆ : Jul. 26 ; ▲ : Aug. 3 ; ★ : Aug. 30 ; ● : Sep. 22 ; ▼ : Oct. 25.

species was in the range of 800 to 1,200% (Fig. 4). The optimum was equal to the optimum of the same species measured the year before (Ino and Takamine, 1994). When the water content was lower than 800%, the photosynthetic rate dropped sharply, and when higher than 1,200%, it decreased gently. These relations correlated with the following polynomial equations and the curves are shown in Fig. 4 :

*S. tenellum* ; $\mathbf{Pn} = -0.0004\mathbf{Wc}^4 + 0.0882\mathbf{Wc}^3 - 3.30\mathbf{Wc}^2 + 40.6\mathbf{Wc} - 60.8$ (3)
$R^2 = 0.905$

*S. papillosum* : $\mathbf{Pn} = -0.00007\mathbf{Wc}^2 + 0.162\mathbf{Wc} + 9.87$ (4)
$R^2 = 0.797$

*S. nemoreum* ; $\mathbf{Pn} = 0.0071\mathbf{Wc}^4 - 0.155\mathbf{Wc}^3 - 0.652\mathbf{Wc}^2 + 28.7\mathbf{Wc} - 37.2$ (5)
$R^2 = 0.926$

where Pn is the relative rate (%) to the maximum net photosynthetic rate and Wc is the water content to dry weight.

3. Seasonal changes of the maximum photosynthetic rates

The maximum photosynthetic rate and respiration rate in each month are shown in Fig. 5. The photosynthetic rate and respiration rate of *S. tenellum* in

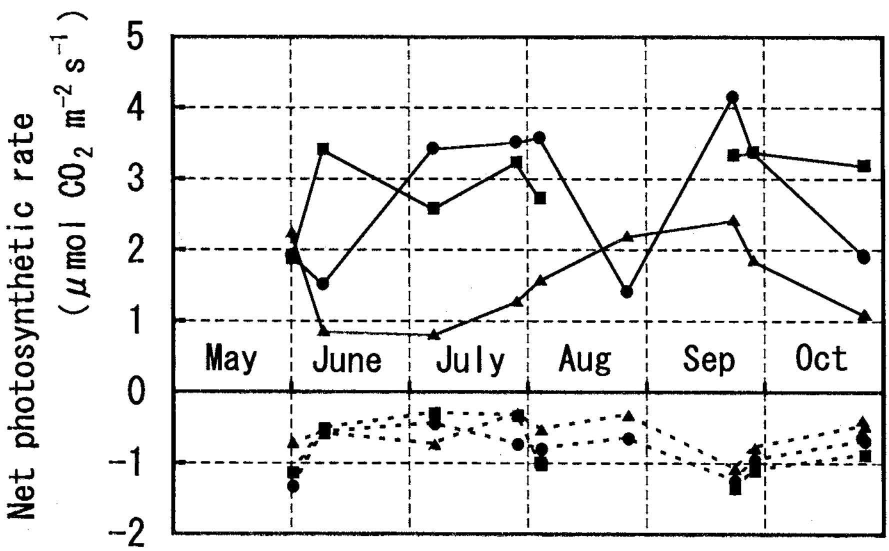



Fig. 5. Seasonal changes of the maximum net photosynthetic rates and dark respiration rates at 25°C of *Sphagnum tenellum* (■), *S. papillosum* (●) and *S. nemoreum* (▲).

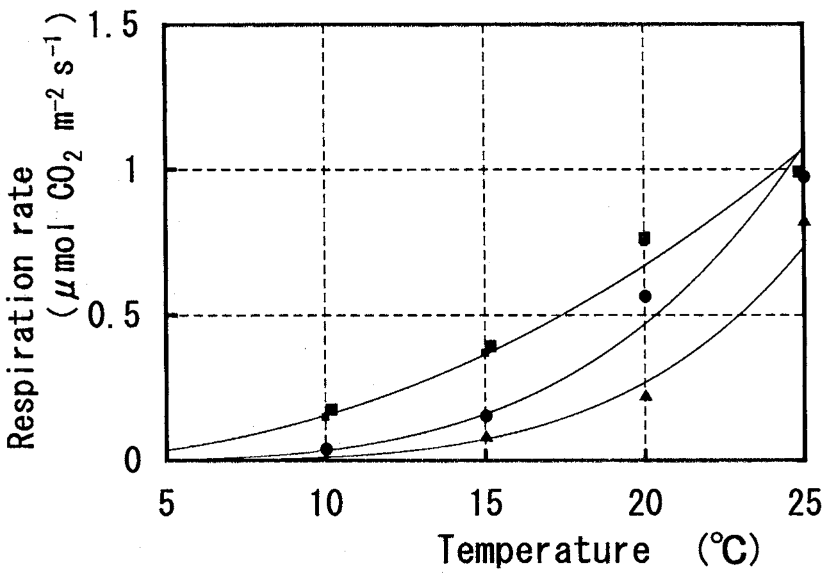



Fig. 6. The relationships between the moss temperature and the respiration rate of nonphotosynthetic layer.
■ : *Sphagnum tenellum*, ● : *S. papillosum*, ▲ : *S. nemoreum*.

Table 1. Days of calculation, net production and respiration of 3 species of *Sphagnum*.

| Month | Days | | | Net production rate under optimum water content (a) (g dw m$^{-2}$ month$^{-1}$) | | | Corrected production rate by daily water content (b) (g dw m$^{-2}$ month$^{-1}$) | | | Respiration rate of nonphotosynthetic layer (c) (g dw m$^{-2}$ month$^{-1}$) | | | (b)−(c) (g dw m$^{-2}$ month$^{-1}$) | | | Correct/optimum (b)/(a) (%) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *S.t.* | *S.p.* | *S.n.* | *S.t.* | *S.p.* | *S.n.* | *S.t.* | *S.p.* | *S.n.* | *S.t.* | *S.p.* | *S.n.* | *S.t.* | *S.p.* | *S.n.* | *S.t.* | *S.p.* | *S.n.* |
| 1990 May | 07-31 | | 07-31 | 53 | | 35 | 48 | | 35 | 12 | | 3 | 35 | | 31 | 90 | | 99 |
| 1990 June | 01-30 | | 01-30 | 95 | | 42 | 80 | | 41 | 35 | | 16 | 45 | | 25 | 85 | | 97 |
| 1990 July | 01-31 | | 01-31 | 62 | | 100 | 49 | | 96 | 54 | | 31 | −4 | | 66 | 79 | | 96 |
| 1990 August | 01-31 | | 01-31 | 61 | | 63 | 50 | | 60 | 49 | | 36 | 1 | | 24 | 82 | | 95 |
| 1990 September | 01-30 | | 01-30 | 70 | | 81 | 62 | | 76 | 27 | | 17 | 34 | | 59 | 88 | | 94 |
| 1990 October | 01-13 | | 01-13 | 39 | | 16 | 34 | | 15 | 5 | | 1 | 29 | | 14 | 87 | | 94 |
| Total | 160 | | 160 | 380 | | 337 | 323 | | 322 | 182 | | 104 | 141 | | 219 | 85 | | 96 |
| 1991 May | 31-31 | 31-31 | 31-31 | 3 | 0 | 2 | 3 | 0 | 2 | 1 | 0 | 0 | 2 | 0 | 1 | 98 | | 100 |
| 1991 June | 01-30 | 01-30 | 01-30 | 96 | 11 | 43 | 85 | 11 | 42 | 29 | 20 | 16 | 56 | −9 | 26 | 89 | 100 | 98 |
| 1991 July | 01-31 | 01-31 | 01-31 | 71 | 16 | 90 | 60 | 15 | 86 | 36 | 27 | 25 | 23 | −12 | 61 | 84 | 95 | 95 |
| 1991 August | 01-31 | 01-31 | 01-31 | 79 | 54 | 65 | 69 | 53 | 63 | 39 | 31 | 30 | 31 | 22 | 33 | 88 | 97 | 97 |
| 1991 September | 01-30 | 01-30 | 01-30 | 43 | 47 | 91 | 37 | 41 | 89 | 24 | 15 | 13 | 13 | 26 | 77 | 87 | 87 | 98 |
| 1991 October | 01-11 | 01-11 | 01-11 | 26 | 6 | 12 | 21 | 6 | 11 | 5 | 1 | 1 | 16 | 5 | 10 | 81 | 100 | 95 |
| Total | 134 | 134 | 134 | 317 | 134 | 303 | 275 | 126 | 293 | 134 | 94 | 85 | 141 | 32 | 207 | 88 | 96 | 97 |
| 1993 May | 13-31 | 13-31 | 13-31 | 35 | 30 | 23 | 31 | 30 | 22 | 8 | 1 | 3 | 23 | 29 | 20 | 90 | 100 | 97 |
| 1993 June | 01-30 | 01-30 | 01-30 | 84 | 19 | 42 | 75 | 19 | 40 | 22 | 6 | 12 | 53 | 13 | 29 | 90 | 100 | 94 |
| 1993 July | 01-31 | 01-31 | 01-31 | 70 | 20 | 61 | 61 | 19 | 49 | 37 | 18 | 24 | 23 | 1 | 24 | 86 | 97 | 80 |
| 1993 August | 01-31 | 01-31 | 01-31 | 74 | 57 | 66 | 65 | 56 | 57 | 36 | 16 | 23 | 29 | 40 | 34 | 87 | 98 | 87 |
| 1993 September | 01-30 | 01-30 | 01-30 | 71 | 48 | 84 | 63 | 48 | 74 | 23 | 6 | 10 | 40 | 42 | 64 | 89 | 100 | 89 |
| 1993 October | 01-18 | 01-18 | 01-18 | 51 | −17 | 19 | 42 | −17 | 17 | 4 | 0 | 0 | 38 | −17 | 16 | 82 | 100 | 89 |
| Total | 159 | 159 | 159 | 385 | 157 | 294 | 337 | 155 | 259 | 131 | 48 | 72 | 206 | 107 | 187 | 87 | 99 | 89 |

*S.p.*: *Sphagnum papillosum* *S.t.*: *S. tenellim* *S.n.*: *S. nemoreum*

August were not measured. The photosynthetic rates in September were higher than in other months. The respiration rates in September and late in May were higher than in other months.

4. Respiration in nonphotosynthetic layer

There were good correlations in the relationships between the respiration rate and the moss temperature in all species (Fig. 6). Respiration was not detected at 5°C and the rate rose sharply with the increase of the temperature.

These relationships were shown as the following equations:

*S. tenellum* ; $\mathbf{Rd}=0.0012\mathbf{Tm}^{2.109}$ $R^2=0.989$ (6)

*S. papillosum* ; $\mathbf{Rd}=0.0143\mathbf{Tm}^{1.6164}$ $R^2=0.996$ (7)

*S. nemoreum* ; $\mathbf{Rd}=0.0001\mathbf{Tm}^{3.6942}$ $R^2=0.996$ (8)

where **Rd** is the dark respiration rate and **Tm** is the moss temperature at 0.5 cm depth.

Hourly respiration rates in their habitats were calculated with hourly mean moss temperature at Takadayachi moor. Daily respiration rates were calculated as the sum of hourly rates and they are shown in Table 1. Their range was 131 to 182 gdw$m^{-2}$ $y^{-1}$ in *S. tenellum*, 48 to 94 g $m^{-2}$ $y^{-1}$ in *S. papillosum* and 72 to 104 g $m^{-2}$ $y^{-1}$ in *S. nemoreum*.

5. Calculation of net production under the optimum water content

Matter production was calculated with the equation (1) and (2) in growing season, May to October, in 1990, 1991 and 1993. The photosynthesis in *S. tenellum* was not measured in August. Therefore the components $p_n$ and $q_n$ in the equations of August were estimated from the regression equations in July and September. The calculation in the periods when PFD or the moss temperature was not recorded was not done. Annual net production rate in the optimum water content was 136 to 157 gdw$m^{-2}$ $y^{-1}$ in *S. papillonum*, and 317 to 385 g $m^{-2}$ $y^{-1}$ in *S. tenellum*, and 294 to 337 g $m^{-2}$ $y^{-1}$ in *S. nemoreum*, respectively.

6. Estimation of the water content in the habitat

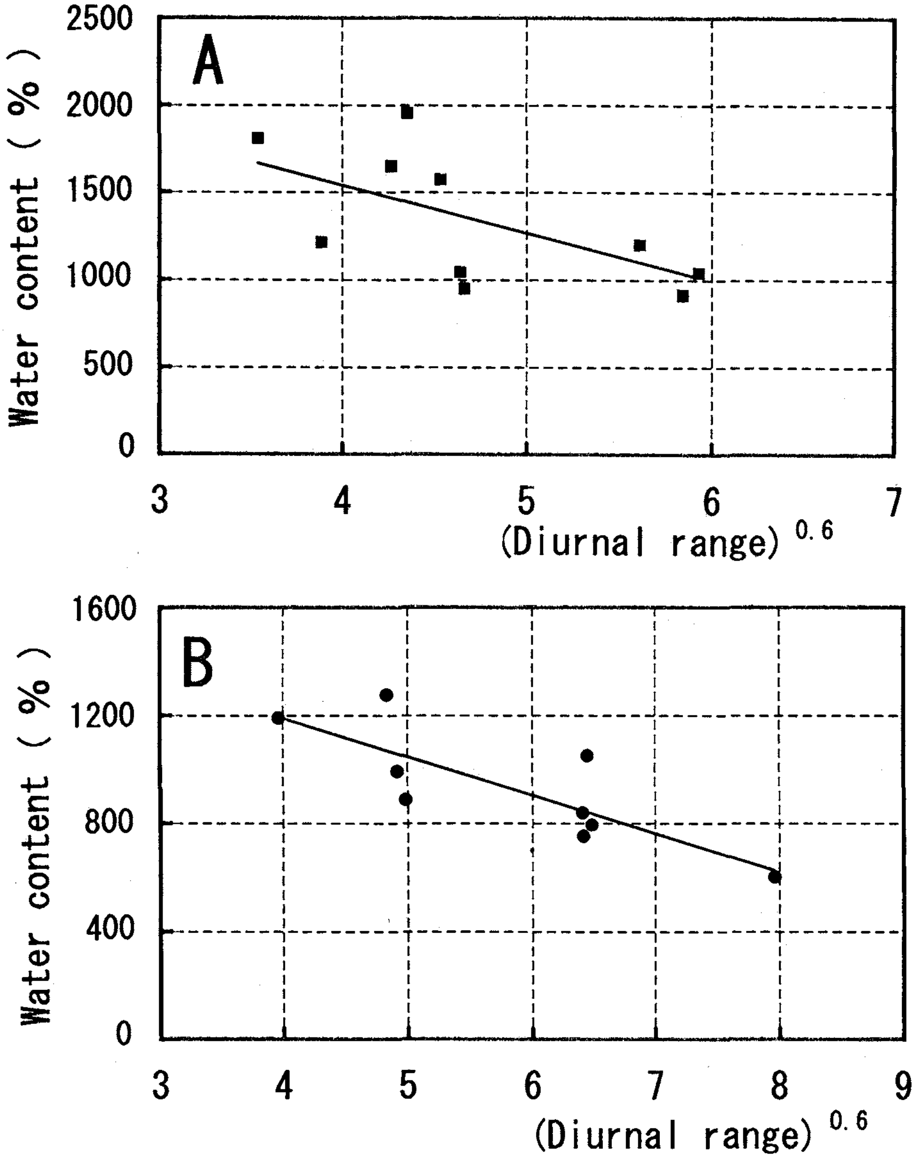
The relationhips between the diurnal range of the moss temperature and the water content of the shoots are shown in Fig. 6. The following equations were got by using the relationships:

*S. tenellum* ; $\mathbf{Wc}=-2.73\mathbf{DR}+26.3$ $R^2=0.311$ (9)

*S. papillosum* ; $\mathbf{Wc}=-1.42\mathbf{DR}+17.6$ $R^2=0.648$ (10)

*S. nemoreum* ; $\mathbf{Wc}=-1.21\mathbf{DR}+16.2$ $R^2=0.442$ (11)

where **Wc** is the water content of shoots and **DR** is the 0.6 power of the diurnal range of the moss temperature.




DISCUSSION

The photosynthetic rate of moss is controlled by the water content as shown in Fig. 4. The water content of *Sphagnum* in the habitat was affected by the climate and the water table. The water content in the habitat was not always under the optimum condition. Therefore the production rate which was calculated with the photosynthetic rate under the optimum water condition is over the

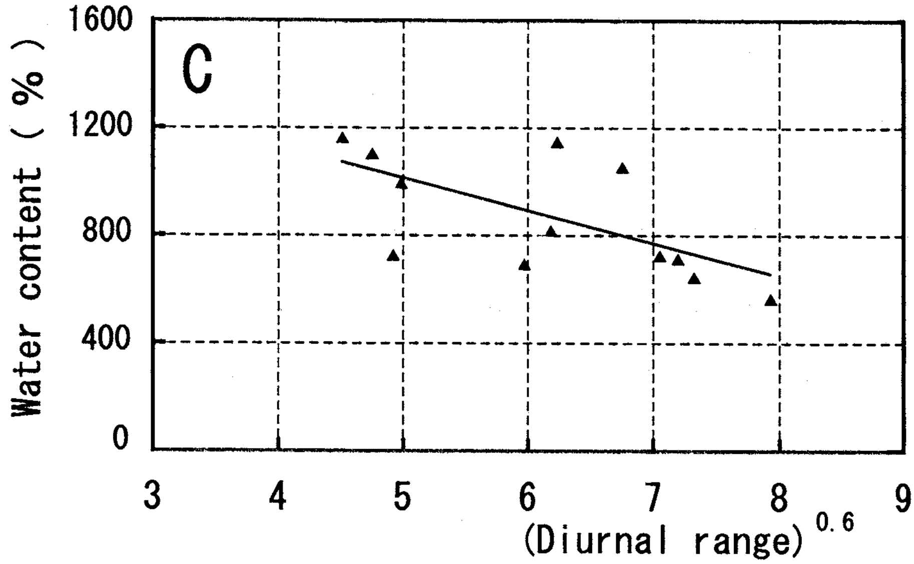



Fig. 7. The relationship between the diurnal range of the moss temperature and the water content of mosses.
A : *Sphagnum tenellum*, B : *S. papillosum*, C : *S. nemoreum*.

actual rate. If the daily water content in the habitat can be estimated, the daily net production rate under the optimum water condition can be corrected with the equations (3) to (5).

If the water content of photosynthetic layer is high, the change of moss temperature in the layer is made small by the evapotranspiration in daytime and the heat capacity of water at night. Therefore, it is estimated that as the water content gets higher, the diurnal range of the moss temperature becomes smaller and as the water content gets lower, the diurnal range, larger. The relation shown in Fig. 7 supports the above estimation. The daily mean water content of photosynthetic layer could be estimated with the diurnal range of the temperature in the layer. The production rates calculated under the optimum water condition were corrected with the equations (9) to (11) and equations (3) to (5). As shown in Table 1, the corrected production rates (b) of *S. tenellum* growing in the hollows were lower than 90% of the production rates (a). *S. papillosum* growing in the hummocks was not largely affected by the water content and the corrected production rates were 96 to 99% of those in the optimum water content. The decrease in the production of *S. nemoreum* in the hummoks was small in 1990 and 1991, but in 1993, it increased to about 12% of the optimum rate.

Another correction was carried out about the respiration of nonphotosynthetic layer. The dry matter amount per day used by the respiration of that layer was calculated with the equations (6) to (8). It was considered that the daily mean moss temperature of the layer was equal to the daily mean air temperature. The annual production rates which is gained by subtracting the respiration (c) from the production rate (b) are shown in Table 1. That rate ((b)−(c)) was 141-206 gdw$m^{-2}$, 32-107 g $m^{-2}$ and 187-219 g $m^{-2}$ in *S. tenellum*, *S. papillosum* and *S. nemoreum*, respectively. The measurement periods of the microclimate were shorter than the growing periods from thaw to snowfall. Therefore it seems that these calculated rates were slightly lower than the actual annual production rates of these mosses.

There were some reports that the net production rates of *S. papillonum* amounted 66 to 610 g $m^{-2}$ $y^{-1}$ (Clymo, 1970; Kashimura, 1982; Kashimura and Kantani, 1987; Lindholm and Vasander, 1990; Moor, 1989). We could not find the production rates of *S. tenellum* and *S. nemoreum*.

## SUMMARY

Photosynthesis of *Sphagnum tenellum*, *S. papillosum* and *S. nemoreum* were measured monthly under the optimum water contents in their growing season of 1989. These species were dominant in Takadayachi moor of Hakkoda Mts. in northern part of Honshu. *S. tenellum* is growing in the hollows and others are in the hummocks. The surface layer temperature of each moss population and photon flux density (PFD) were measured and recorded with some loggers. The dry matter production in photosynthetic layer of each species was calculated with the relation between photosynthetic rate and moss temperature, PFD and the water content. Then the respiration of nonphotosynthetic layer was subtracted from the dry matter production. The ranges of the dry matter accumulations in growing seasons of 1990, 1991 and 1993 were 141-206 g $m^{-2}$, 32-190 g $m^{-2}$ and 187-219 g $m^{-2}$ in *S. tenellum*, *S. papillosum* and *S. nemoreum*, respectively.

## REFERENCES

Clymo, R.S. 1970. The growth of *Sphagnum*: Methods of measurement. J. Ecol., **58**, 13-49.

Clymo, R.S. 1973. The growth of *Sphagnum*: Some effects of environment. J. Ecol., **61**, 849-869.

Clymo, R.S. and Hayward, P.M. 1982. The ecology of *Sphagnum*. In "Bryophyte ecology" ed. Smith, K.J.E. p. 229-289. Chapman and Hall, London.

Dilks, T.J.K. and Proctor, M.C.F. 1979. Photosynthesis, respiration and water content in bryophytes. New Phytol., **82**, 97-114.

Grigal, D.F. 1984. *Sphagnum* production in forested bogs of northern Minnesota. Can. J. Bot., **63**, 1204-1207.

Harley, P.C., Tenhunen, J.D., Murray, K.J. and Beyers, J. 1989. Irradiance and temperature effects on photosynthesis of tussock tundra *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. Oecologia, **79**, 251-259.

Ino, Y. and Takamine, Y. 1994. The measurement of photosynthesis in four *Sphagnum* mosses for three high moors at Mt. Hakkoda (Japanese). Gakujutsu Kenkyu (Academic Studies), Biology. Geology, XXXXII: 1-9.

Kappen, L., Meyer, W. and Bölter, W. 1988. Photosynthetic production of the lichen *Ramalina terebrata* Hook f. et Tayll., in the maritime Antarctic. Polarfoschung, **58**, 181-188.

Kashimura, T. 1982. Production and decomposition of *Sphagnum* mats in Shimotashiro-Ukishima area, Ozegahara Moor. Conservation and restoration of Ozegahara Moor XII, 41-49.

Kashimura, T. and Kantani, J. 1987. Structure and development of the surface layer of a bog in Akaiyachi Moor. (Japanese). Report of the Nature of Lake Inawashiro, 11-16, Fukushima Univ.

Kashimura, T. and Tachibana, H. 1982. The vegetation of the Ozegahara Moor and its conservation. Ozegahara : Scientific Research of the Highmoor in Central Japan, 193-224.

Lindholm, T. and Vasander H. 1990 Production of eight species of *Sphagnum* at Suurisuo mire, southern Finland. Ann. Bot. Fenn., **27**, 145-157.

Moor, T.R. 1989. Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada. Can. J. Bot., **67**, 1203-1207.

Pakarinen, P. 1987. Production and nutrient ecology of three Sphagnum species in south Finnish raised bogs. Ann. Bot. Fenn., **15**, 15-26.

Rochefort, L., Vitt, D.H. and Bayley, S.E. 1990. Growth, production and decomposition dynamics of *Sphagnum* under natural and experimentally acidified condition. Ecology, **71**, 1986-2000.

Russel, S. 1984. Growth measurement in bryophytes : A case study. J. Hattori Bot. Lab., **56**, 147-157.

Rydin, H. and McDonald, J.S. 1985. Photosynthesis in *Sphagnum* at different water contents. J. Bryol., **13**, 579-684.

Tachibana, H., Sasahara, K. and Tsugihara, S. 1987. A preliminary report of the production of Sphagna in the central part of Furen mire, eastern Hokkaido. (Japanese). Nagano-ken Shokubutsu Kenkyuu-kai Shi, 20, 31-35.

Titus, J.E. and Wagner, D.J. 1984. Carbon balance for two *Sphagnum* mosses : Water balance resolves a physiological paradox. Ecology, **65**, 1765-1774.

Titus, J.E., Wagner, D.J. and Stephens, M.D. 1983. Contrasting water relations of photosynthesis for two *Sphagnum* mosses. Ecology, **64**, 1109-1115.

Yoshioka, K. 1963. Ecological studies of the Takadayachi Moor in the Hakkoda Mountains 1. General aspects of the environment and vegetation. Ecol. Rev., **16**, 13-26.

Wallen, B., Falkengren-Grerup, U. and Malmer, N. 1988. Biomass, productivity and relative rate of photosynthesis of *Sphagnum* at different water levels on a South Swedish peat bog. Holarct. Ecol., **11**, 70-76.

Wieder, R.K. and Lang, G.E. 1983. Net primary productivity of the dominant bryophytes in a *Sphagnum*-dominated wetland in West Virginia. Bryologist, **86**, 280-286.