Response Patterns of Net Photosynthesis to Moisture of Mosses in Xeric Habitats

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The response patterns of net photosynthesis to moisture level of mosses in xeric habitats were compared with those in mesic habitats, in order to determine whether the former species are better adapted to the xeric condition with regard to carbon gain.

Moss species examined were *Rhacomitrium lanuginosum* and *R. barbuloides* in xeric open habitats and *Dicranum japonicum*, *Hypnum plicatulum*, *Ptilium crista-castrensis*, *Pleurozium schreberi* and *Hylocomium splendens* in mesic habitats on the coniferous forest floor in the upper subalpine zone of Mt. Fuji. Three additional xerophytic species collected at other localities, *Ptychomitrium polyphylloides*, *Grimmia pilifera* and *Hedwigia ciliata*, were also examined.

Five species in the xeric habitats showed an optimum range of moisture level for net photosynthesis, 2 to 3 $g \cdot g^{-1}$. On the other hand, species in the forest showed a wider optimum range, 3 to 8 $g \cdot g^{-1}$. Net photosynthetic rate at the moisture level of 0.5 $g \cdot g^{-1}$ was positive in xerophytic mosses, but negative in most forest mosses.

Moisture levels where external capillary water disappeared and drop of water potential began was determined by blotting water-saturated shoots with membrane filters. These moisture levels were low in the xerophytic mosses and high in the forest mosses, although there were some exceptions.

It was concluded that mosses in xeric habitats are better adapted for the efficient use of water for photosynthesis than those in mesic habitats.

Key words: Adaptation — Moisture — Moss — Net photosynthesis — Water potential — Xeric habitat.

It is well known that water availability is one of the most important factors that limit distribution and productivity of bryophytes. Although the majority of bryophyte species are restricted to moist or wet habitats, some species grow mostly in open dry habitats, where they are exposed to frequent severe desiccation. These xerophytic species must have developed several physiological adaptations to desiccation.

The degree of desiccation tolerance of bryophyte and its recovery in activity after rehydration are directly related to the ability to colonize in xeric habitats. Some experimental studies have shown that xerophytic bryophytes can survive a long desiccation period and recover their photosynthetic activity rapidly after rehydration (Dilks and Proctor, 1974; Alpert and Oechel, 1985; Streusand *et al.*, 1986).

In addition to this physiological tolerance to desiccation, the response pattern of photosynthesis to moisture level in shoots may have a considerable influence on the

ability to colonize in xeric habitats, since it is directly related to the carbon economy of bryophytes. Several authors have examined the differences in the response patterns of net photosynthesis to moisture level between species of different habitats (Oechel and Collins, 1976; Dilks and Proctor, 1979). They showed that species in relatively dry habitats have lower optimum moisture level for net photosynthesis than those in constantly wet habitats, and suggested that the response patterns of photosynthesis to moisture in bryophytes are adapted to the water availablility in their habitats. However, in xeric habitats where bryophytes experience repeated wetting and drying, their production process is largely affected by the pattern of water supply and water loss. Therefore, ecological importance of the response patterns of net photosynthesis to moisture level in xerophytic bryophytes must be investigated in relation to natural fluctuations in water condition.

In the present study, we examine the differences in the response patterns of net photosynthesis to moisture level between typical moss species in xeric habitats and those in mesic forest floor. Ecological meaning of the differences in these patterns is discussed in relation to the fluctuation patterns in water condition observed in the field.

Materials and Sites

Seven moss species used in the present study were collected at Oniwa, northwestern slope in the upper subalpine zone (2300-2400 m alt.) of Mt. Fuji (35°23′N, 138°43′ E). This area is composed of open lava field, scrub of *Larix leptolepis* and coniferous forest dominated by *Tsuga diversifolia* and *Abies veitchii*. The composition and structure of moss communities in this area were studied in relation to the forest succession by Nakamura (1984). The monthly mean air temperatures of June, July, August and September 1986, measured at ca. 30 cm above the ground in the lava field, were 9.2, 12.4, 12.6 and 10.0 C, respectively.

Moss species collected at Oniwa included *Rhacomitrium lanuginosum*, *R. barbuloides*, *Hypnum plicatulum*, *Ptilium crista-castrensis*, *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum japonicum*. *R. lanuginosum* was the dominant species of the open lava field. *R. barbuloides* was also common in open sites, but it was mostly found in less xeric habitats such as partially shaded sites near shrubs or vertical surface of rock. *Hypnum plicatulum* was widely found in the coniferous forest and was abundant on the barks of trees and on rotten logs. *Ptilium crista-castrensis* was mostly found at the edge of the forest. *Pleurozium schreberi* and *Hylocomium splendens* dominated on the coniferous forest floor making large mats. *Dicranum japonicum* was also common on the forest floor but grew in patches.

Other xerophytic species, *Ptychomitrium polyphylloides*, *Grimmia pilifera* and *Hedwigia ciliata* were also examined. *P. polyphylloides* and *G. pilifera* were collected at Hikawa in Tokyo (35°48′N, 139°06′E; 300-400 m alt.), and *H. ciliata* was collected at Nippara in Tokyo (35°51′N, 139°02′E; ca. 700 m alt.). *P. polyphylloides* grew on a concrete wall. *G. pilifera* and *H. ciliata* were found on the south-facing surface of dry

rock.

Methods

All samples were stored in a growth box at 10 C under a 12L/12D photoperiod pending measurements. The photosynthetic photon flux density (PPFD) during the light period was ca. 100 μmol m^{-2} s^{-1}. The measurements of net photosynthesis were usually carried out within a week after collection. The green (living) portion of the shoots was cut and placed on a round plate of nylon net 9 cm in diameter at the original density and orientation. These samples were wetted with distilled water one day before the measurements.
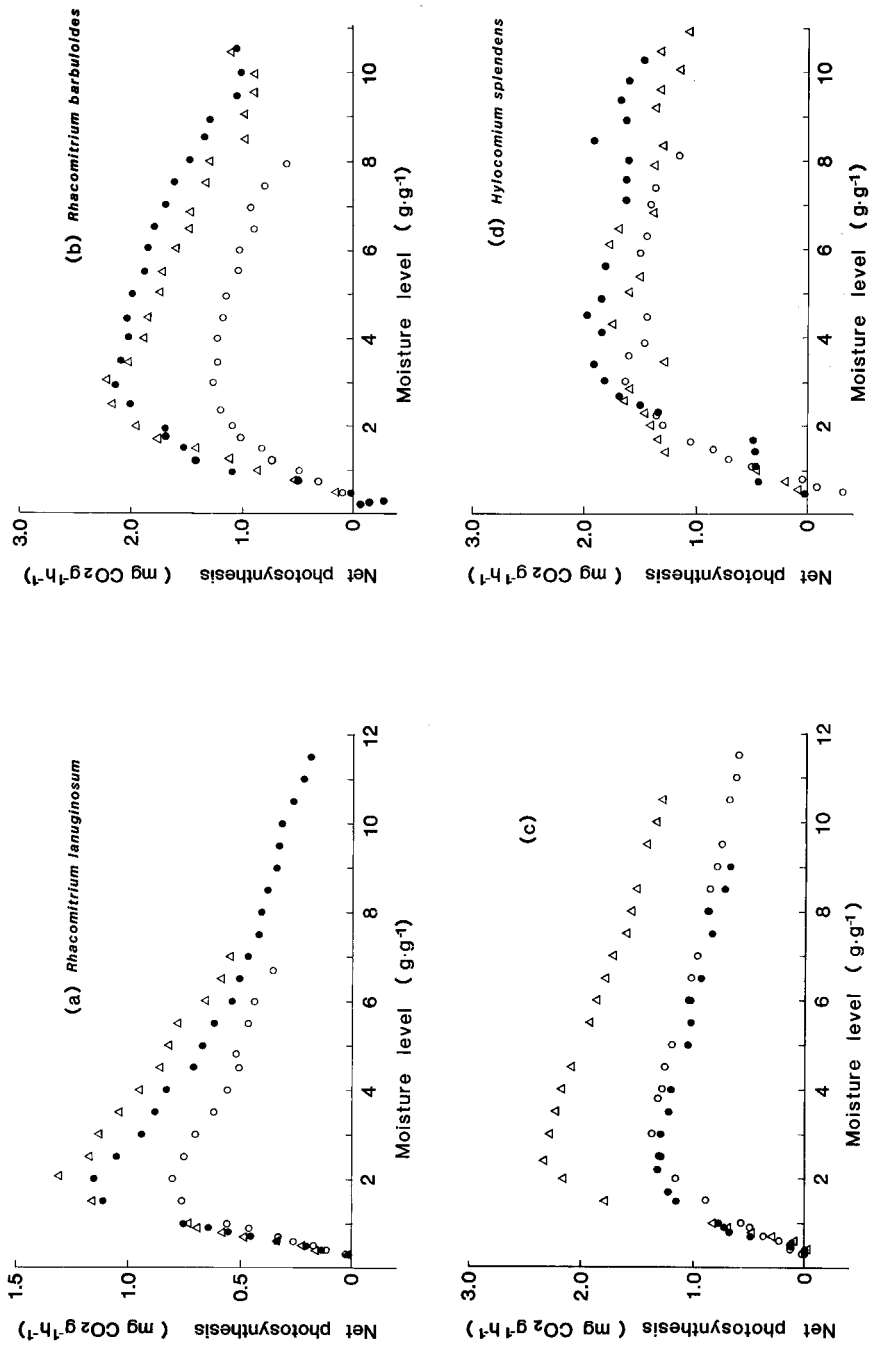
Net photosynthesis was measured using an open circuit gas exchange system with an infrared gas analyzer (Koito MC-D3A) and a temperature-regulated assimilation chamber with a volume of 3 l (Koito MC-A3). The two plates with moss shoots were placed in the chamber. Moss tissue temperature was monitored with a chromel-alumel thermocouple and was adjusted to 10 C during the measurement. Radiation provided by a metalhalide lamp (Mitsubishi M700C-BOC-U) was filtered through a water filter 6 cm deep and a white net. Unless otherwise noted, PPFD at the moss surface level was fixed at 800 μmol m^{-2} s^{-1} during the measurement. The flow rate of the air was 2 l min^{-1}, and the relative humidity of the air was 80 to 87%. Under this condition, the moss samples gradually lost their water. The samples were taken out from the chamber at an interval of 30 min (forest species) or one hour (xerophytic species) for measurement of their fresh weights. Gas exchange measurement was continued until the fresh weight of the sample became nearly constant. Time needed for each gas exchange measurement was 2 to 5 hr in forest species and 4 to 13 hr in xerophytic species.

After the gas exchange measurements, the samples were dried to a constant weight at 80 C to obtain the dry weight. The moisture level of the sample at any point was calculated assuming linear decrease in moisture level during the intervals between the measurements of fresh weight. The moisture level of the sample was expressed as gram weight of water per one gram of moss dry weight:

$$\text{Moisture level } (\text{g} \cdot \text{g}^{-1}) = \frac{\text{Fresh weight (g)} - \text{Dry weight (g)}}{\text{Dry weight (g)}}$$

"Moisture level" in the present study is a synonym for "water content" in most of the literature on bryophytes (cf. Dilks and Proctor, 1979). However, since this value includes the weight of external capillary water at high moisture level, we use the term "moisture level" to distinguish it from water content of the cells.

Moisture level where external capillary water disappeared and drop of water potential began was determined as follows. Moss shoots, 0.1 to 0.7 g in dry weight, were dipped in distilled water to be saturated with water. Most of the external water was removed from the moss surface with filter papers. These shoots, after being blotted with membrane filters (pore size=0.45 μm) until no more water could be

(a) *Rhacomitrium lanuginosum*

(b) *Rhacomitrium barbuloides*
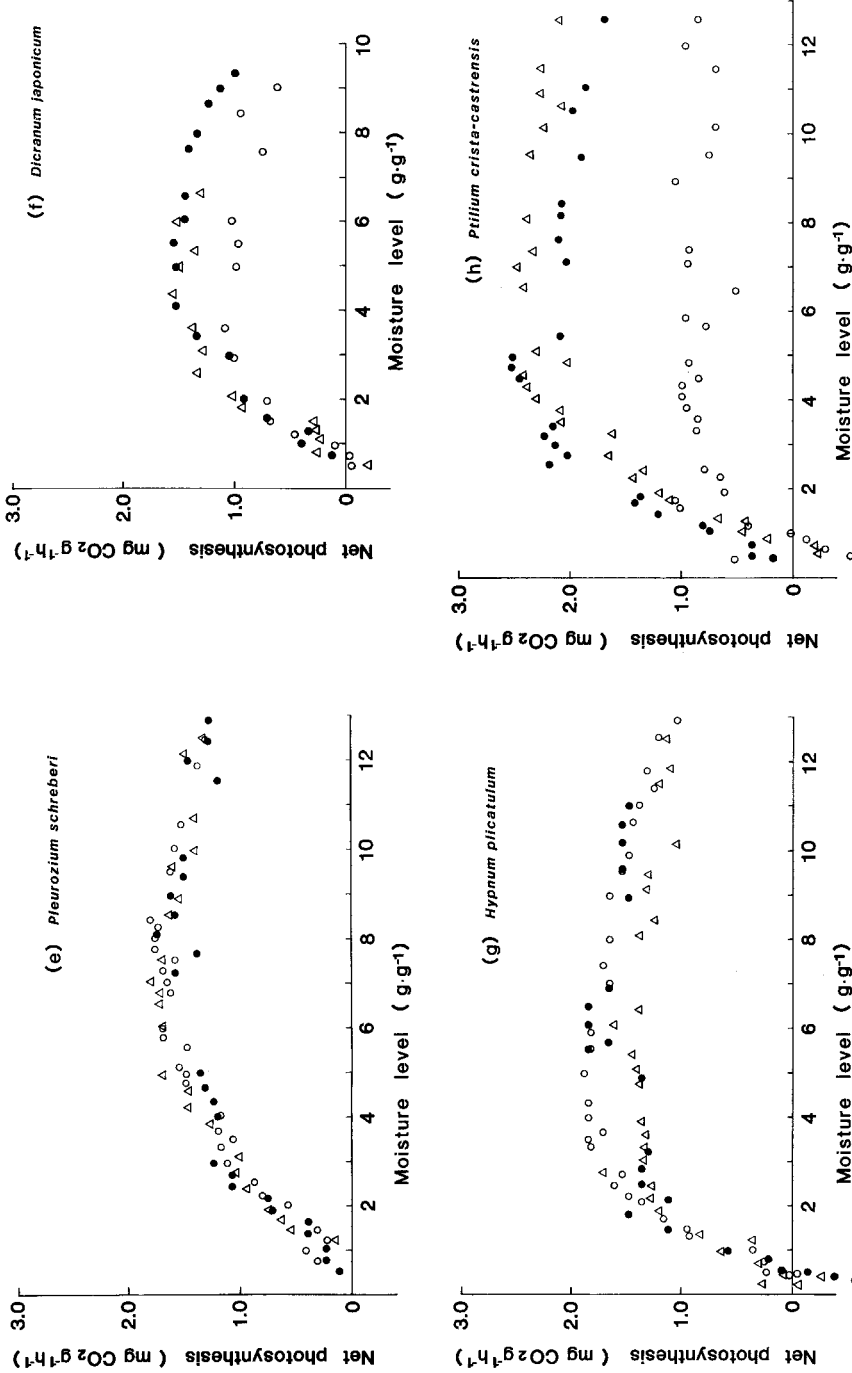
(c)

(d) *Hylocomium splendens*

Fig. 1. Response curves of net photosynthesis to moisture level in mosses. a: *Rhacomitrium lanuginosum*. ○ 9 July, ● 11 Oct., △ 9 Nov. b: *Rhacomitrium barbuloides*. ○ 2 June, ● 9 July, △ 19 Aug. c: ○ *Ptychomitrium polyphylloides*, ● *Grimmia pilifera*, △ *Hedwigia ciliata*. 23 Feb. d: *Hylocomium splendens*. ○ 9 July, ● 23 July, △ 26 Sep. e: *Pleurozium schreberi*. ○ 9 May, ● 2 June, △ 26 Sep. f: *Dicranum japonicum*. ○ 2 June, ● 19 Aug., △ 16 Oct. g: *Hypnum plicatulum*. ○ 2 June, ● 23 July, △ 16 Oct. h: *Ptilium crista-castrensis*. ○ 19 Aug., ● 26 Sep., △ 16 Oct.

withdrawn, were weighed.   External capillary water can be removed by this method because capillary spaces on the moss surface are larger than a few μm across (Proctor, 1982).

Water potentials of moss shoots were measured with a dew point microvoltmeter (Wescor HR-33T) and a sample chamber.

Results

Response patterns of photosynthesis to moisture level

Fig. 1a to 1c show the response curves of net photosynthesis to moisture level in five xerophytic mosses.

Rhacomitrium lanuginosum (Fig. 1a) showed a clear optimum moisture level for net photosynthesis at ca. 2 g•g^{-1}, which is within the optimum range reported for this species (Tallis, 1959 ; Kallio and Heinonen, 1973).   Seasonal shift of this optimum moisture level was not detected, although the maximum rate of photosynthesis varied among three samples collected in different months.   The net photosynthetic rate increased gradually as the shoot lost the water from the saturation point to this optimum moisture level, and it dropped rapidly as the moisture level decreased further. When the moisture level was higher than 7 g•g^{-1}, the rate was less than 50% of the maximum.   Positive net photosynthesis was detected until the moisture level fell below 0.4 g•g^{-1}.

R. barbuloides (Fig. 1b) showed the optimum moisture level for net photosynthesis at ca. 3 g•g^{-1}.   The maximum rate of net photosynthesis was almost twice as high as that of *R. lanuginosum*.   At a moisture level lower than 0.5 g•g^{-1}, net photosynthesis became negative, which means the predominance of respiration over gross photosynthesis.

Ptychomitrium polyphylloides, *Grimmia pilifera* and *Hedwigia ciliata* (Fig. 1c) responded similarly to moisture.   Net photosynthesis of these species reached the maximum rate at a moisture level between 2 and 3 g•g^{-1}, and was negligible at 0.4 g•g^{-1}.

The response curves of net photosynthesis to moisture level in the forest mosses are shown in Fig. 1d to 1h.

Hylocomium splendens (Fig. 1d) showed the optimum range in moisture level from 3 to 6 g•g^{-1}, which agrees with the data reported by Busby and Whitfield (1978).   The optimum moisture levels determined under the PPFD of 150, 300 and 500 μmol m^{-2} s^{-1} were also within this range (Data, not shown).   The suppression of net photosynthesis at a higher moisture level than the optimum was less pronounced in this species than in *R. lanuginosum* ; the net photosynthetic rate at 10 g•g^{-1} was more than 60% of the maximum.   Net pnotosynthesis sometimes became negative at a moisture level lower than 0.7 g•g^{-1}.

Pleurozium schreberi (Fig. 1e) showed an optimum moisture level within the range from 6 to 8 g•g^{-1}, which is higher than the range from 3 to 6 g•g^{-1} reported by Busby and Whitfield (1978).

Table 1. Moisture level of mosses after blotting with membrane filters (pore size = 0.45 μm)

Species	Moisture level (g·g^{-1})
Rhacomitrium lanuginosum	1.33 ± 0.01
R. barbuloides	1.66 ± 0.08
Ptychomitrium polyphylloides	1.96 ± 0.08
Grimmia pilifera	1.52 ± 0.05
Hedwigia ciliata	1.54 ± 0.06
Hylocomium splendens	1.80 ± 0.10
Pleurozium schreberi	1.87 ± 0.05
Dicranum japonicum	1.46 ± 0.07
Hypnum plicatulum	2.09 ± 0.12
Ptilium crista-castrensis	2.20 ± 0.08

Each value is the mean of triplicate determinations ± one standard error.

The other forest species, *Dicranum japonicum* (Fig. 1f), *Hypnum plicatulum* (Fig. 1g) and *Ptilium crista-castrensis* (Fig. 1h) showed similar optimum ranges of moisture between 3 and 8 g·g^{-1}. Negative net photosynthesis was sometimes detected at low moisture levels.

Relationships between moisture level and water potential

Moisture level after blotting with membrane filters was within the narrow range from 1.3 to 2.2 g·g^{-1} for all species examined (Table 1). This moisture level was always lower than the optimum level for net photosynthesis of each species. There seems to be a trend that these moisture levels are low in the xerophytic species and high in the forest species. However, *P. polyphylloides* and *D. japonicum* did not conform to this trend.
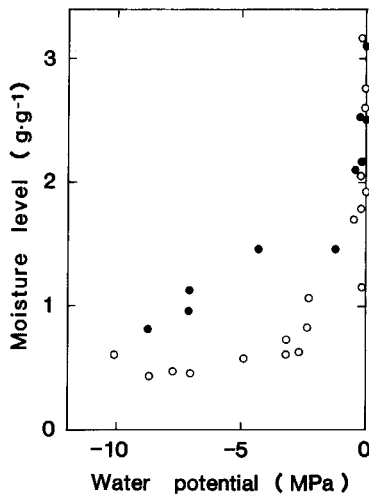

Fig. 2. Relationships between water potential and moisture level.
○ *Rhacomitrium lanuginosum*,
● *Pleurozium schreberi*.

The relationships between moisture level and water potential of the shoots were examined for *R. lanuginosum* and *P. schreberi* (Fig. 2). Water potential of *R. lanuginosum* remained almost zero until the moisture level fell below 2 g·g^{-1}. In the moisture range lower than 1 g·g^{-1}, the water potential dropped rapidly as the moisture level decreased. In *P. schreberi*, measurable drop of water potential began at ca. 2 g·g^{-1}. The decline of water potential with decreasing moisture level was gradual as compared with that of *R. lanuginosum*. At a moisture level lower than 2 g·g^{-1}, water potential was lower in *P. schreberi* than in *R. lanuginosum*.

Discussion

Response patterns of photosynthesis to moisture level and water potential

There is a marked difference in the response pattern of net photosynthesis to moisture level between moss species in xeric habitats and those in forest floor; the former species showed clear optimum moisture levels for net photosynthesis which varied from 2 to 3 g·g^{-1} with species, while the latter species showed wide optimum ranges of high moisture level. Most of the reported values of the optimum moisture level in xerophytic mosses (Dilks and Proctor, 1979; Alpert and Oechel, 1985) and forest mosses (Busby and Whitfield, 1978; Tobiessen et al., 1979) are similar to those obtained in the present study.

The response patterns of net photosynthesis to moisture level in mosses can be explained as follows. At a higher moisture level than the optimum, liquid water is present on the surface and it restricts photosynthesis because of the high diffusion resistance of CO_2 in the liquid phase. When the moisture level is lower than the optimum, moss tissue is dehydrated and photosynthesis is suppressed for lack of water in the protoplasm (Stålfelt, 1938; Dilks and Proctor, 1979; Tobiessen et al., 1979). This explanation agrees with the observation that the moisture level after the removal of external capillary water was always lower than the optimum (Table 1). Since a capillary of 0.45 μm in diameter is equivalent to a water potential of -0.67 MPa, the water potential of moss shoots after the blotting is not more than this value. The trend that moisture levels after the blotting were lower in the xerophytic mosses suggests that the difference in the optimum moisture level is partly due to the difference in the relationship between moisture level and water potential in shoots. However, the exceptions to this trend, *Ptychomitrium polyphylloides* and *Dicranum japonicum*, show that the relationship between net photosynthesis and water potential differs with species. Dilks and Proctor (1979) reported that the relationships between the moisture level and water potential of species in dry habitats are considerably different from those of species in wet habitats; i.e., in the former species, full turgor is reached at the moisture level below 2.5 g·g^{-1} and further water make little difference to water potential, while in the latter species, the major proportion of water is held within the cell and water loss quickly causes depression in water potential. A similar difference was observed between *Rhacomitrium lanuginosum* and *Pleurozium schreberi* in the present study; water potential was lower in the latter species at a moisture level
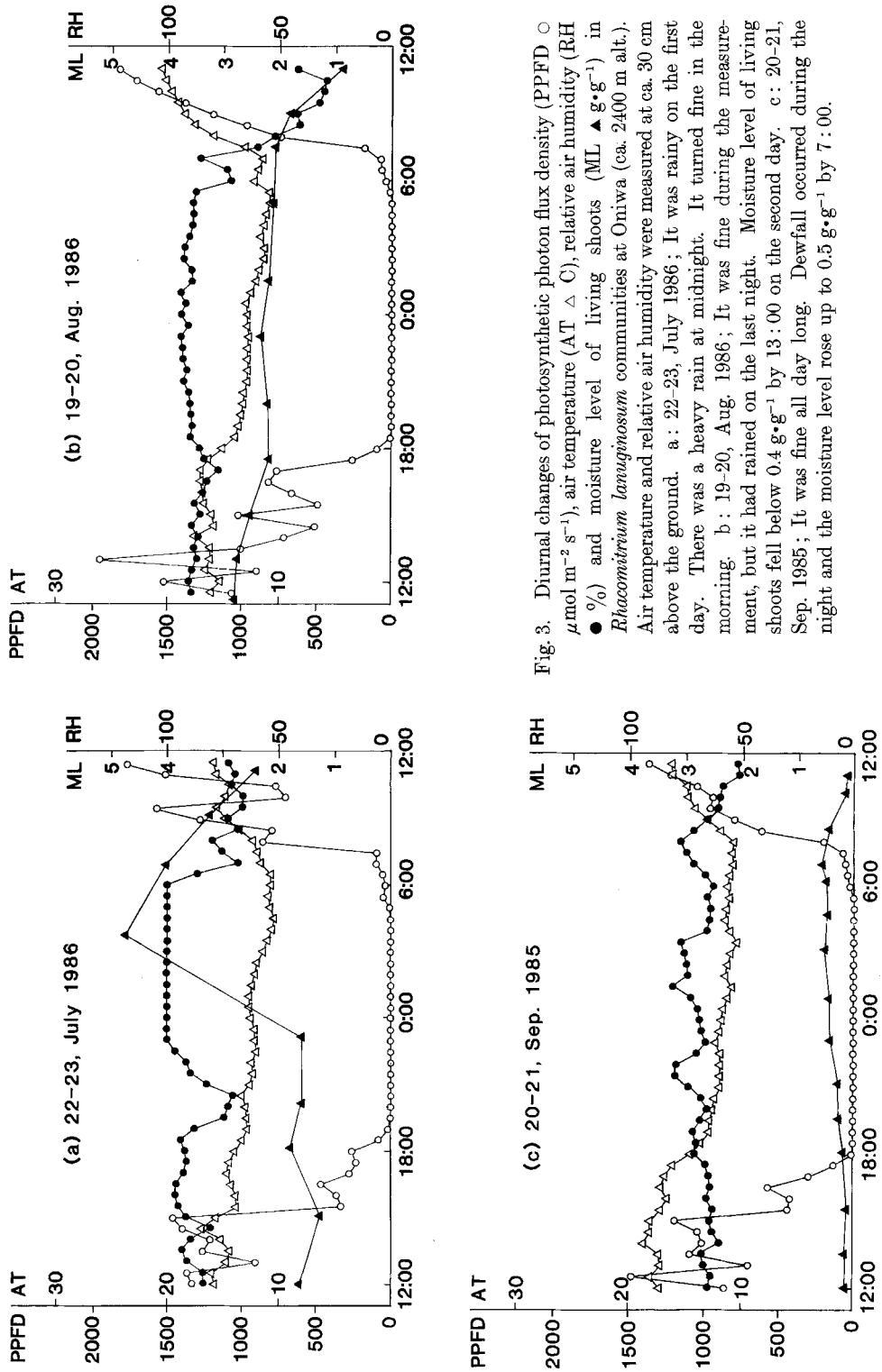
Fig. 3. Diurnal changes of photosynthetic photon flux density (PPFD ○ μmol m^{-2} s^{-1}), air temperature (AT △ C), relative air humidity (RH ● %) and moisture level of living shoots (ML ▲ g·g^{-1}) in *Rhacomitrium lanuginosum* communities at Oniwa (ca. 2400 m alt.). Air temperature and relative air humidity were measured at ca. 30 cm above the ground. a : 22–23, July 1986 ; It was rainy on the first day. There was a heavy rain at midnight. It turned fine in the morning. b : 19–20, Aug. 1986 ; It was fine during the measurement, but it had rained on the last night. Moisture level of living shoots fell below 0.4 g·g^{-1} by 13 : 00 on the second day. c : 20–21, Sep. 1985 ; It was fine all day long. Dewfall occurred during the night and the moisture level rose up to 0.5 g·g^{-1} by 7 : 00.

lower than 2 g•g⁻¹ (Fig. 2). However, in *P. schreberi*, drop of water potential could not detected until the moisture level became considerably lower than the optimum. The cause of this contradictory result is probably that the thickness of the water film on the moss surface was not uniform and dehydration of protoplasm began while extracellular water was partially present. This nonuniform thickness of water film may also be responsible for the wide optimum water range for net photosynthesis and for the unclear suppression of photosynthesis at higher moisture levels in the forest mosses.

Ecological importance of the response patterns of net photosynthesis to moisture in xeric habitats

Water condition of mosses in xeric habitats can be characterized by short-term fluctuation in moisture level and short wetting period available for photosynthesis. Some examples of diurnal change in microclimates and the moisture level of the *R. lanuginosum* community at the study site in Oniwa are shown in Fig. 3a to 3c. On rainy days when relative humidity of the air was near 100%, the moisture level of the community was largely affected by precipitation; the moisture level of the living shoots was around 1.5 g•g⁻¹ when it drizzled, but it rose up to 4 g•g⁻¹ during a heavy rain (Fig. 3a). After a rainfall, moisture level of the community decreased gradually; the decreasing rate was relatively slow on cloudy days or during the night, but when the weather turned fine, the rate was accelerated by intense solar radiation and low relative humidity of the air (Fig. 3b). Once the environment dried up, community moisture level was usually lower than 0.3 g•g⁻¹ during the daytime and its photosynthetic activity was suppressed.

When moss shoots are wetted to near water saturation by a heavy rain, the response patterns of net photosynthesis to moisture level of xerophytic species are disadvantageous because their photosynthesis is considerably suppressed at high moisture levels. However, since excess water can easily drain to surroundings (Dilks and Proctor, 1979) and evaporation rate is usually rapid (Fig. 3a, b), suppression of photosynthesis by excess water may not be a serious problem in most xeric habitats.

On the other hand, when moistened by a small amount of water, the response patterns of net photosynthesis to moisture of xerophytic mosses seem to be advantageous because they maintain relatively high photosynthetic activity at low moisture levels. For example, at 1 g•g⁻¹, the photosynthetic rates of the xerophytic species were at least 40% of the maximum rate, while those of the forest species were less than 30% of the maximum. Even at 0.5 g•g⁻¹, the xerophytic species maintained positive net photosynthesis, while most forest species showed negative net photosynthesis. These facts suggest that the xerophytic mosses are better adapted for the effective use of minor water sources such as fog, dew or drizzle. For example, dewfall may frequently occured in open habitats, but it supplies only a small amount of water to mosses. It is estimated that dewfall during a clear night seldom exceed about 0.5 mm of precipitation (Proctor, 1982). Therefore, response patterns of photosynthesis to moisture level are important for the efficient use of dew as a water source for photosyn-

thesis.

In fact, dew absorption by *R. lanuginosum* was observed at the study site (Fig. 3c). During a clear night, moss surface temperature was usually lower than the air temperature due to the long wave radiation, and condensation of water vapour occurred on the moss surface. As a result, moisture level of mosses increased gradually even when relative humidity of the air was lower than 80%. The moisture level of the living shoots at dawn was sometimes above $0.5 \text{ g} \cdot \text{g}^{-1}$ which would be sufficient for positive net photosynthesis in this species, although it dropped below $0.3 \text{ g} \cdot \text{g}^{-1}$ within a few hours. The facts described above suggest that mosses growing in xeric habitats can be photosynthetically active even in the dry period between rainfalls. They partly compensate for the shortness of wetting periods available for photosynthesis by the efficient use of the minor water sources.

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