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Role of Environmental Conditions in the Habitat Segregation of Two Abundant Vascular Epiphytes in a Warm-Temperate Forest

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Abstract

The relationship between vertical stratification of vascular epiphytes on host trees and epiphyte ecophysiological strategy was examined. We compared the relative growth rate (RGR) of two epiphytic ferns, *Lemmaphyllum microphyllum* and *Lepisorus thunbergianus*, which grow at different canopy positions in warm-temperate forests. The experiment was conducted under two different light and water conditions. In *L. thunbergianus*, the RGR of the leaves and roots were high under high-light conditions, while the mean RGR of the leaves was <0 under low-light conditions. In *L. microphyllum*, the RGR of the leaves was high under high-light conditions. Differences in the water supply did not have significant effects on epiphyte growth. However, *L. microphyllum* showed faster growth than that by *L. thunbergianus* under increased water and light conditions. Different responses of the two epiphyte species to light and water conditions corresponded approximately to their growing position on host trees. The positive influence of high-light conditions and negative influence of low-light conditions on the growth of *L. thunbergianus* demonstrate the importance of light conditions for the growth and survival of the species, which inhabits a relatively bright zone (upper canopy). On the other hand, high growth rate of *L. microphyllum*, which is found at regions ranging from the bottom of the stems to the basal part of the canopy, with increased light and water conditions indicates the importance of the two conditions for the growth and survival of the species.

Key words: Epiphytic fern, Growth rate, Light condition, Vertical distribution within canopy, Warm-temperate forest, Water supply

Introduction

Epiphytic species frequently exhibit different vertical distribution and partitioning of the available space on host tree species (Johansson 1974; Werneck and Espírito-Santo 2002). Different abilities of epiphyte to acclimate to drought and varying light conditions may allow them to coexist at different positions within the same host trees. Habitat segregation among epiphyte species is assumed to have implications on the maintenance of high diversity of these species in forests; thus, the ecophysiology of epiphytes

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has received much attention.

Many studies on epiphyte ecophysiology have focused on tropical rainforest species and have shown that vertical stratification of epiphytes within the canopy is correlated to gradients in humidity, available moisture, and light conditions (Hietz and Briones 1998; Zotz and Hietz 2001). Epiphytic species with high desiccation tolerance were found on highly exposed branches, and species without evident adaptations to drought were found in the most humid and shaded conditions (Hietz and Briones 1998); water supply exerted the strongest influence on epiphyte growth (Laube and Zotz 2003). A few studies have also examined the relationship between vertical stratification of epiphytes and their physiology in tropical dry forests. Graham and Andrade (2004) found that contrary to their hypothesis, epiphytic bromeliads occurring in more exposed canopy locations had lesser drought tolerance than that by other species. Canopies in dry forests tended to be more open than those in tropical rainforests (Zimmerman and Olmsted 1992), and their humidity gradient and exposure are not high (Graham and Andrade 2004). Instead, receiving more rainfall in the exposed locations and rainfall interception in the lower canopy caused by overhead tree branches and leaves (Graham and Andrade 2004) may result in unexpected outcomes in tropical dry forests. The results of previous studies suggest that vertical segregation mechanisms in epiphytes differ according to the surrounding environment and canopy structure. However, the current understanding of epiphyte ecophysiology is highly biased regionally (Werneck and Espírito-Santo 2002), taxonomically, and ecologically (Zotz and Hietz 2001). To understand the manner in which abiotic factors limit epiphyte growth, survival, and coexistence, studies that include a much wider range of regions, taxa, and growing positions are needed (Zotz and Hietz 2001).

Limited information is available on the relationships between vertical stratification of epiphytes and their physiological traits in temperate forests. Because the distribution of vascular epiphytes is tightly associated with moisture availability, their species diversity and abundance is lower in temperate forests than in tropical rain forests (Zotz 2005). Although most tree species have the ability to support epiphytic plants at suitably humid sites (Werneck and Espírito-Santo 2002), with few such sites in temperate forests, only trees with sufficient water-retention capacity support epiphytes (Freiberg 1996). Therefore, vertical segregation of epiphytes on limited suitable host trees in temperate forests is important for the coexistence of epiphyte species. However, only limited information is available on the specific ecophysiological traits that enable epiphyte segregation in temperate forests.

To examine the relationship between vertical stratification and ecophysiological trait of epiphytes in the warm-temperate forests of Japan, we compared the growth of two epiphyte species found in different canopy positions under different light and water conditions. On the basis of our experimental results, we discuss the role of vertical environmental gradients in the segregation of the two epiphyte species.

Materials and methods

1. Study site and plant distribution

Field measurements were performed at the Kyushu Chuo Sanchi Semi-National Park, southwestern Japan. The study area is in an old-growth evergreen broad-leaved forest. Between 1999 and 2009, the mean annual rainfall was 2472.3 mm, and the mean annual temperature was 17.2°C at the Saito Weather Station. In 1989, a permanent 4-ha plot (200 m × 200 m) was set up on a north to northwest-facing slope on Mt. Omori (1109 m asl; 32° 04' N, 131°09' E) at an elevation of 380-520 m (Sato et al. 1999). This plot has been used for long-term ecological research, and species name, diameter at breast height (DBH; 1.3 m), and location of all trees with DBH greater than 5 cm have been recorded for this site

(Sato et al. 1999). In 2007, we established an 80 × 120 m plot within the permanent 4-ha plot. We recorded the species and the growing positions of all adult epiphytes on 283 trees with DBH greater than 20 cm. On the basis of the revised zonation scheme described by Johansson (1974), epiphyte growing position was classified into five types: basal part of the trunk (0-2 m); trunk from 2 m to the first ramification; basal part of the canopy (basal third of the total branch length); middle part of the canopy (middle third of total branch length); and outer part of the canopy (outer third of total branch length). The distribution pattern and composition of vascular epiphytes in this forest have been described previously (Hirata et al. 2009). Excluding the accidental epiphyte species, 8 orchids, 13 pteridophytes, and 2 mistletoes were recorded.

We selected two of the most common epiphytic ferns, *Lemmaphyllum microphyllum* and *Lepisorus thunbergianus*, and compared their distributions in the canopy. *L. microphyllum* is a creeping fern, whereas *L. thunbergianus* is an erect fern. Although long-term climate data are lacking for all growing positions, instantaneous photosynthetic photon flux density (PPFD) values (measured using photometric sensors [Quantum Light Sensor 3668I, Spectrum Technologies, Inc., Plainfield, IL] connected to data loggers [WatchDog 200; Spectrum Technologies, Inc., Plainfield, IL]) in our study site indicate that light supply increased from the stem bottom to the canopy branching point. The mean relative PPFD (RPPFD) during the daytime was 0.1% at the stem bottom and 3.7% at the branching point. The maximum RPPFD value was 0.9% at the stem bottom and 16.7% at the branching point. Humidity was measured using a miniature hygrometer (Hygrochron, KN Laboratories, Inc., Osaka, Japan) in August 2009 for growing positions 2, 3, and 4 because many epiphyte species occur at these growing positions (Hirata et al. 2009). Throughout the observation period, humidity was higher at the stem bottom than at the branching point (Fig. 1).

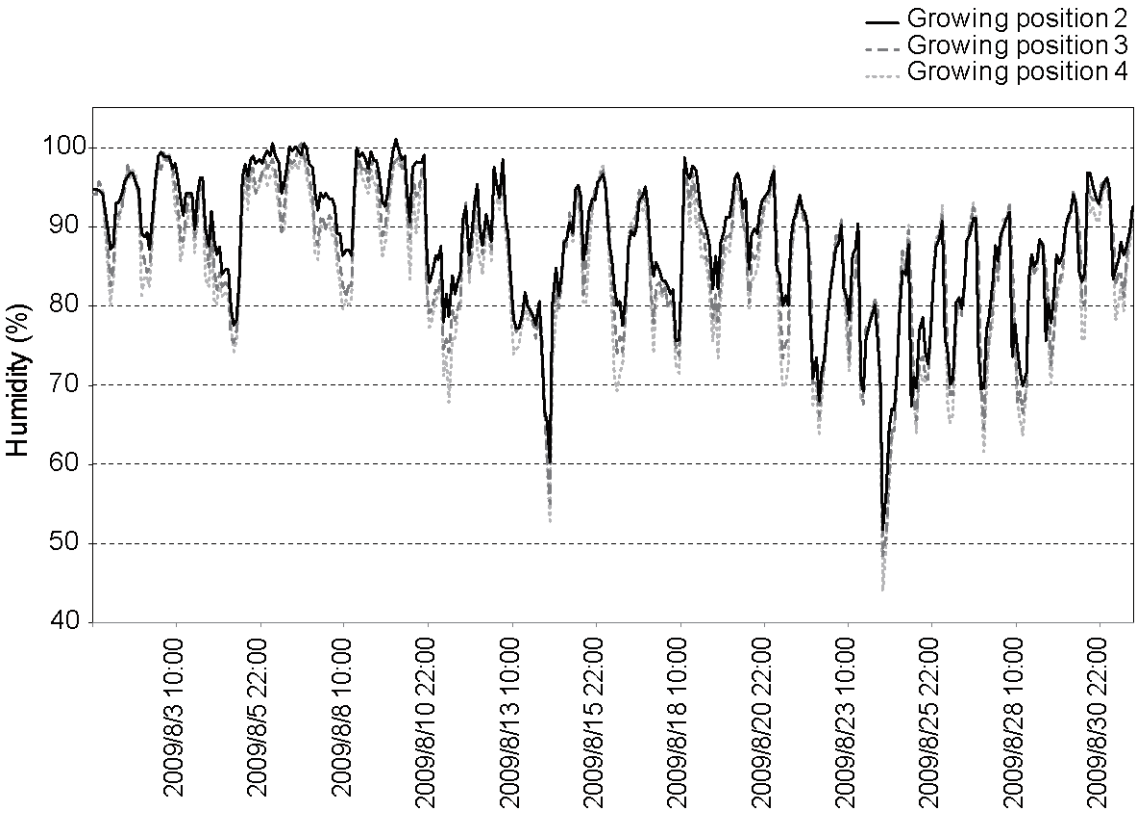


Fig. 1 Humidity at Growing positions 2, 3 and 4 in August 2009. Growing position 2 is the trunk from 2 m up to the first ramification; Growing position 3 is the basal part of the canopy (basal third of total branch length); Growing position 4 is the middle part of the canopy (Site 4, middle third of total branch length).

2. Plant collection and treatment

We collected approximately 48 individuals of each species from the field site in June 2009. Individual plants were planted in plastic pots with pumice soil and kept in a greenhouse at the University of Tsukuba for two months under neutral-density shade cloth which provided approximately 50% ambient PPFD. Water was supplied every three days. It is difficult to distinguish an individual *L. microphyllum* because of its creeping form. Therefore, we defined an individual as a plant part with rhizome meristems and more than 30 leaves. After two months, we measured the leaf and root lengths of all plants.

3. Growth experiment and data analysis

The growth experiment was conducted from August 2009 to February 2010. We used two different light and water conditions: high light (L+; approximately 75% of direct sunlight) and low light (L-; approximately 10% of direct sunlight); and high watering (W+; watered once every three days) and low watering (W-; watered once every five days). There were 10 replicates per treatment ($n = 4 \times 10$ individuals per species) for each species. Under the W+ condition, the soil surface was rarely dry, whereas under the W- condition, the soil surface was dry for more than two days. All plants were provided with the same amount of fertilizer every 15 days. At the beginning of the experiment, no significant difference was observed in plant size between the treatments ($P > 0.05$, Kruskal-Wallis test). After approximately six months, we measured the length and width of leaves and the length of roots. Leaf area of fresh leaves was determined using Lia32 image-analysis software (http://www.agr.nagoya-u.ac.jp/%7Eshinkan/LIA32). We also measured the dry weight of leaves and roots separately for each species.

The response variable in the growth experiment was relative growth rate (RGR) ($g \cdot g^{-1} \cdot d^{-1}$), which is defined as follows:

$$RGR = (\ln DW_{end} - \ln DW_{initial})/\Delta t,$$

where, DW is plant dry weight and Δt is the duration of the experiment in days (Evans 1972). Unhealthy and particularly small individuals at the beginning of experiment were removed from the growth analysis. We evaluated RGR separately for the leaves and roots by using formulas from a preliminary experiment. The initial DW of the leaves and roots was estimated from measured leaf length (L_l), leaf width (L_w), root length (R_l), and root width (R_w) as follows:

For *L. microphyllum*,

$DW_{leaf} = 7.53e^{-5} \times A_{est} + 2.60e^{-2}$ ($R^2 = 0.87$, $P < 0.001$),

$DW_{root} = 3.98e^{-4} \times R_l + 4.63e^{-3}$ ($R^2 = 0.84$, $P < 0.001$),

$A_{est} = L_l/2 \times L_w/2 \times \pi$.

The leaf shape of *L. microphyllum* differs between sterile and fertile leaves, and the ratio of leaf width to length for fertile leaves is smaller than that of sterile leaves. Therefore, we used the leaf length and width to estimate the DW_{leaf} in *L. microphyllum*.

For *L. thunbergianus*,

$DW_{leaf} = 7.71e^{-4} \times L_l - 6.82e^{-2}$ ($R^2 = 0.90$, $P < 0.001$),

$DW_{root} = 1.70e^{-3} \times R_l \times R_w + 2.39e^{-2}$ ($R^2 = 0.70$, $P < 0.001$),

Because the thickness of *L. thunbergianus* roots varied between individuals regardless of the root length, DW_{root} correlated more strongly with the formula that used both the root length and width than that using only the root length ($R^2 = 0.53$, $P < 0.001$). Therefore, we used the root length and width to estimate DW_{root} in *L. thunbergianus*.

A two-way ANOVA was performed to test the effects of light and water conditions on the growth of each species. We also tested the effects of light and water conditions on changes in the leaf mass per area (LMA $g \cdot g^{-1} \cdot d^{-1}$) for each species by using a three-way ANOVA. All statistical analyses were performed using R 2.15.2 (R Core Team 2012).

Results

L. microphyllum and *L. thunbergianus* were distributed across different growing positions in the canopy. *L. microphyllum* was generally

found on the lower parts of host trees, whereas *L. thunbergianus* was found on the higher and exposed parts of host trees (Fig. 2).

The growth rates of both the species were consistently low. The highest RGR values were, respectively, 0.009 and 0.007 $g \cdot g^{-1} \cdot d^{-1}$ for *L. microphyllum* leaf and root and 0.018 and 0.007 $g \cdot g^{-1} \cdot d^{-1}$ for *L. thunbergianus* leaf and root.

The RGR of the leaves of both the species grown under high-light conditions was higher than of those grown under low-light conditions (Fig. 3, Table 1). The RGR of *L. thunbergianus* roots grown under high-light conditions was higher than that under low-light and high-water conditions. Differences in the water supply did not have significant effects on epiphyte growth; however, *L. microphyllum* had higher leaf growth when grown under high-water and high-light conditions (Fig. 3). In *L. thunbergianus*, the mean RGR of leaves was <0 when grown under low-light conditions (Fig. 3).

Changes in the biomass allocation patterns differed between the two species (Fig. 4). In *L. microphyllum*, the leaf/root ratio was higher in plants grown under the high-light and high-water conditions than that under the low-light and low-water conditions. In *L. thunbergianus*, the leaf/root ratio was higher in plants grown under the high-light and high-water conditions

Table 1 Results of a two-way ANOVA of the effects of light(L) and water(W) on relative growth rate (RGR) after the growth experiment.

Factor	DF	*F*	*P*
Lemmaphyllum microphyllum (leaves)			
L	1	14.97	< 0.001
W	1	0.52	0.48
L:W	1	3.30	0.08
Residuals	26		
Lemmaphyllum microphyllum (roots)			
L	1	2.27	0.14
W	1	0.61	0.44
L:W	1	1.01	0.32
Residuals	26		
Lepisorus thunbergianus (leaves)			
L	1	37.24	< 0.001
W	1	0.67	0.42
L:W	1	0.15	0.70
Residuals	34		
Lepisorus thunbergianus (roots)			
L	1	5.16	0.03
W	1	0.10	0.76
L:W	1	0.21	0.65
Residuals	34		

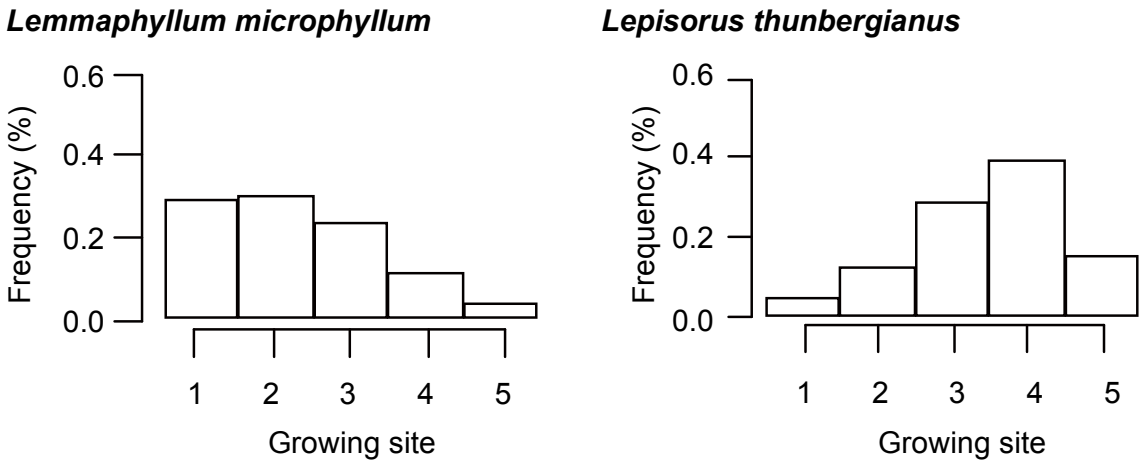


Fig. 2 Distribution of two epiphytic ferns in host trees in a Japanese warm-temperate forest. Frequency indicates occurrence frequency of each epiphyte species on each growing position of 283 host trees in the study plot. Growing positions are: the basal part of the trunk (Growing position 1, 0-2 m); the trunk from 2 m up to the first ramification (Growing position 2); the basal part of the canopy (Growing position 3, basal third of total branch length); the middle part of the canopy (Growing position 4, middle third of total branch length); and the outer part of the canopy (Growing position 5, outer third of total branch length).

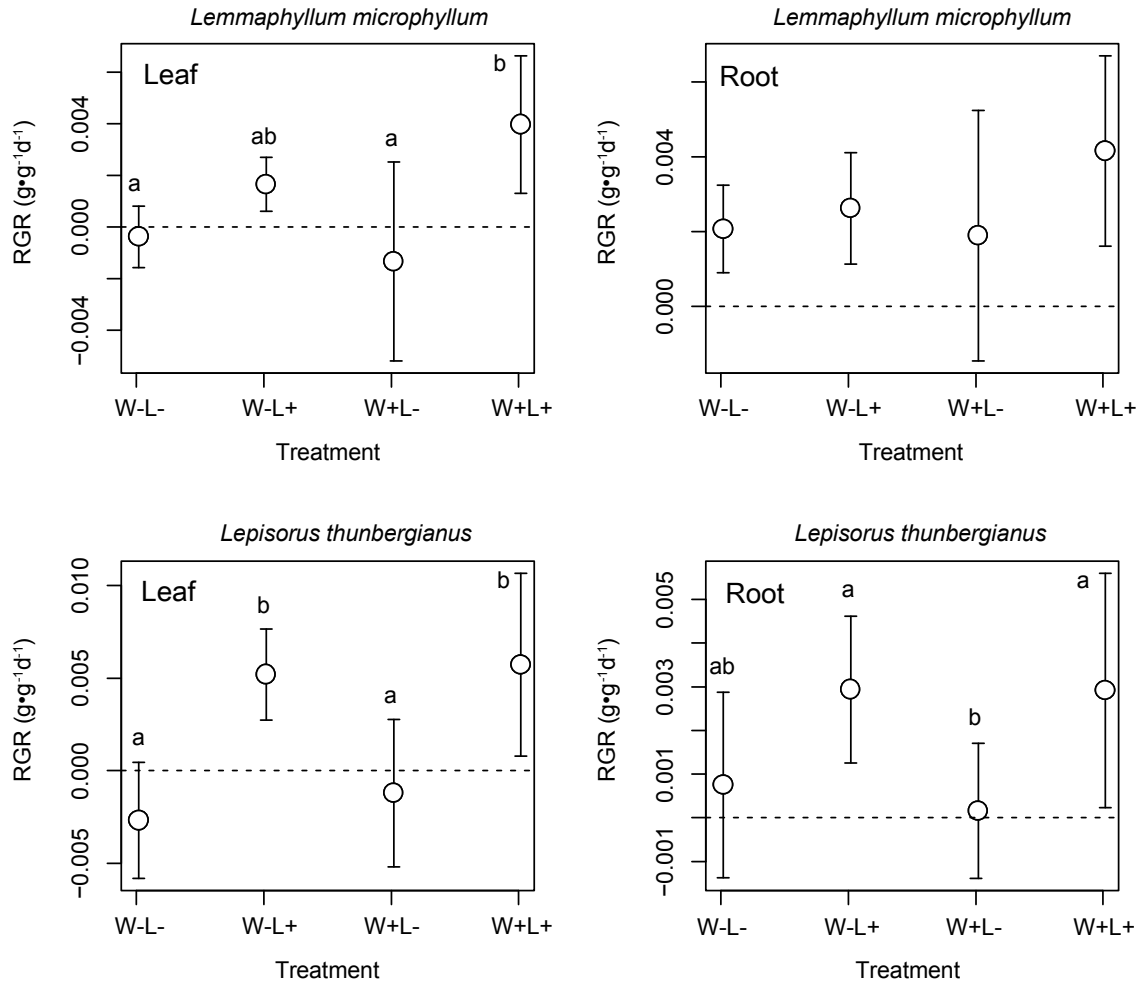


Fig. 3 Response of relative growth rate (RGR) to varying levels of water (W) and light (L) supply. Data are *means* ± *SD*. The two levels of resource supply are indicated as low (-) and high (+). Different letters indicate significant differences among treatments (Tukey post-hoc test, $P < 0.05$).

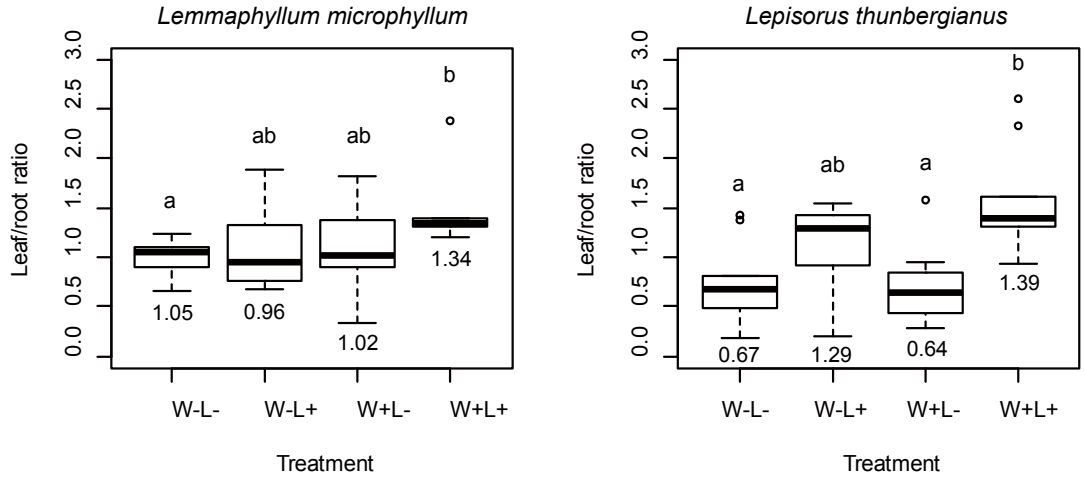


Fig. 4 Leaf/root ratio under varying levels of water (W) and light (L) supply. The two levels of resource supply are indicated as low (-) and high (+). Different letters indicate significant differences among treatments (Steel-Dwass multiple comparison test, $P < 0.05$). The numbers below the boxplots indicate the median value.

than that under the low-light and low-water or high-light and low-water conditions. Under the low-light conditions, median leaf/root ratio of *L. thunbergianus* was <1.

The effect of different light conditions on LMA was statistically significant in both the

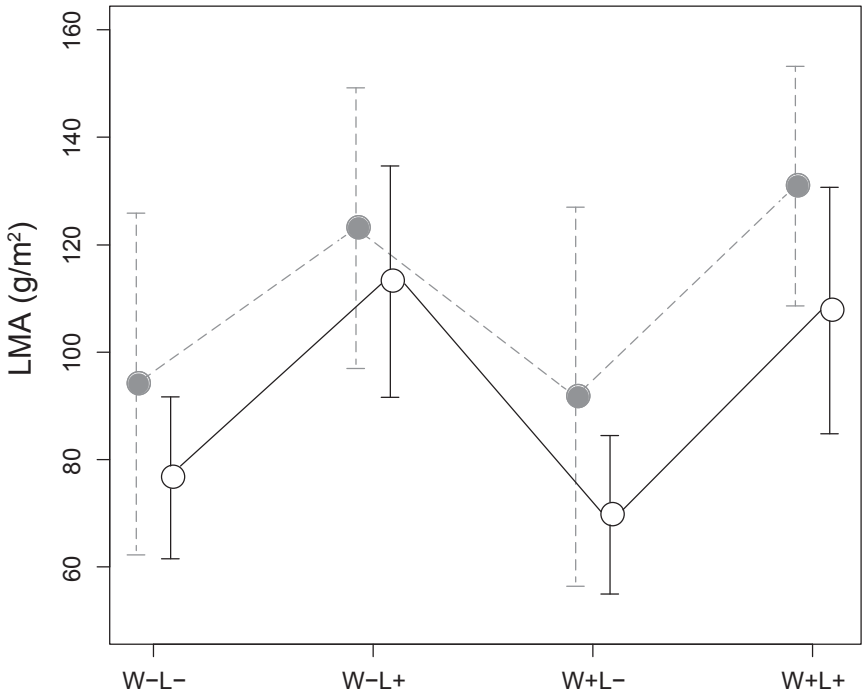


Fig. 5 Response of leaf mass area (LMA) to varying levels of water (W) ant light (L) supply. Gray dashed lines and filled circles indicate results for *Lepisorus thunbergianus* and black lines and open circles indicate results for *Lemmaphyllum microphyllum*. Data are *means* ± *SD*. The two levels of resource supply are indicated as low (-) and high (+).

species (Fig. 5, Table 2). High-light conditions increased LMA in both the species. The mean LMAs in *L. thunbergianus* were larger than those in *L. microphyllum* for all the treatments, although the difference in LMA between the two species was statistically significant under the low-light and high-water conditions and high-light and high-water conditions (*t*-test, $P < 0.05$).

Table 2 Results of a three-way ANOVA of the effects of light (L), water (W) and epiphyte species on LMA after the growing experiment.

	DF	*F*	*P*
L	1	51.74	< 0.001
W	1	0.09	0.76
SP	1	13.43	< 0.001
L:W	1	0.43	0.51
L:SP	1	0.09	0.76
W:SP	1	0.80	0.37
L:W:SP	1	0.19	0.66
Residuals	98		

Discussion

The different responses of the two epiphyte species to light and water conditions corresponded approximately to their growing position on the host trees. Increased light supply stimulated growth in both the species. However, this trend was more remarkable in *L. thunbergianus*, which was found in relatively bright and dry locations in the upper canopy (Fig. 3, Table 1). The positive influence of high-light conditions and the negative influence of low-light conditions on the growth of *L. thunbergianus* demonstrate the importance of light conditions in the growth and survival of the species. On the other hand, variations in the water supply did not affect growth of *L. thunbergianus* (Fig. 3, Table 1). Increasing wind speed, radiation, temperature oscillation, and vapor-pressure deficit increase evaporation and transpiration from the stem base to the outer twigs (Parker 1995). Because of these factors, drought stress in epiphytes is more severe in the upper canopy. *L. thunbergianus*, a species typically found in the upper canopy, may have higher drought tolerance. *L.*

thunbergianus had higher RGR under high-light condition regardless of water conditions. Conversely, *L. microphyllum* had higher RGR under high-light and high-water conditions. Such growth responses to drought may contribute to maintaining the high abundance of *L. thunbergianus* in the upper canopy.

The growth rate of *L. microphyllum* was high under high-light and high-water conditions (Fig. 3, Table1). The ability to utilize both the high light and water conditions may be important for the growth and survival of *L. microphyllum*. *L. microphyllum* is generally found at the bottom of the stems to the basal part of the canopy on host trees. In the canopy of host trees in our study site, light and humidity showed opposite trends along the vertical axis. Thus, it is reasonable that at the intermediate position on host trees (upper part of the stems and basal part of the canopy), where *L. microphyllum* may be exposed to moderate light and humidity, is the primary location of *L. microphyllum*. However, *L. microphyllum* was also found at the bottom of the tree stems, which are relatively shaded environments. *L. microphyllum* may be highly shade tolerant, although we did not directly measure its photosynthetic abilities. We found that *L. microphyllum* had thinner leaves than that of *L. thunbergianus*, when grown under high water conditions. Generally, succulence (LMA) increases with light exposure (Hietz and Briones 1998), and plants that are adapted to shade tended to have thinner leaves to avoid maintaining leaf tissue at light conditions below the compensation point (Larcher 1995). Thus, the thinner leaves of *L. microphyllum* when grown under high water conditions suggest that *L. microphyllum* was highly shade tolerant under high water condition. At the stem bottom, addition to the higher humidity than upper canopy (Fig. 1), large volumes of stemflow may be generated during rainfall because of the funneling effect of the tree crown (Herwitz 1987). For instance, Masukata et al. (1990) reported that the stemflow of an evergreen broadleaved tree species *Lithocarpus edulis* was 64% of the rainwater that fell onto its crown. This abundant water supply at the bottom of the tree stems may allow *L. microphyllum* to grown in relatively shaded environments.

Changes in the leaf/root ratio of both species to light and water conditions also differed. *L. thunbergianus* allocated relatively more biomass to the leaves than to the roots under high-light conditions, whereas relatively more biomass was allocated to the roots under low-light conditions. Negative leaf growth of *L. thunbergianus* under low-light conditions may be because of the investment of biomass to the roots, although root growth under low-light and high-water conditions was also lower than that under high-light and high-water conditions (Fig. 3). Morphological adjustments to shade suggest an increase in biomass allocation to aboveground organs and a decrease in biomass allocation to the roots (Poorter and Nagel 2000). However, the opposite response occurred in *L. thunbergianus* allocation. In *L. microphyllum*, allocation to leaf biomass was high in plants grown under high-light and high-water conditions. Biomass allocation was nearly constant in plants grown under other conditions although the variation was large in some treatments. This may suggest that allocation plasticity differs between the two species. *L. thunbergianus*, which is an erect epiphyte, cannot occupy a large area of the host tree by rooting unlike that by *L. microphyllum*, which is a creeping epiphyte. Plasticity in allocation may confer some competitive advantages because the plant can immediately change its allocation strategy according to changes in the environment (Rünk and Zobel 2007).

Graham and Andrade (2004) reported that in a tropical dry forest, drought tolerance had a stronger influence on epiphyte vertical stratification than that by photoprotective ability. They proposed that it was caused by high rainfall and dew at higher locations in the canopy. In this study, the low sensitivity of the two epiphyte species to water supply was an unexpected result, because the vertical humidity gradient and rainwater are high in

closed temperate forests. Our results may have been caused by small differences between the two levels of water supply. In this study, we employed low watering level once every five days, considering the change in substrate from tree bark to pumice soil. Under this treatment, the soil surface remained dry for about three days during each watering period. However, water supply may be more limited under in situ conditions. Thus, it was difficult to compare the relative importance of water or light conditions on epiphyte growth and vertical stratification in this study. On the other hand, *L. microphyllum* showed more sensitive response to water conditions than that by *L. thunbergianus*. Therefore, we assume that water conditions also affect the difference in vertical distribution of the two species.

In this study, we used adult individuals in the growth experiment. However, vertical segregation will be determined at earlier stages, such as at germination and during the growth of young individuals. Previous studies have shown size-dependent responses to environmental conditions (Laube and Zotz 2003; Zotz 2009). Differences in the environmental conditions may strongly affect the establishment and survival of the epiphyte species at early growth stages. Future studies are necessary to examine the effects of light and water conditions on smaller individuals.

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2種の維管束着生植物のすみわけに対する環境要因の役割

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要　旨

ホスト樹木内での着生部位が異なる2種の着生植物、マメヅタとノキシノブを対象に、2段階の光と水条件のもとで生育実験を行い、着生部位の違いと生理生態学的特性との関係を検討した。ノキシノブの葉と根茎の相対成長速度(RGR)は明るい光条件下で高くなり、低い光条件下では葉のRGR平均値は負の値をとった。マメヅタはより明るい光条件下で葉のRGRが高くなった。水条件の違いは2種の成長に有意な影響を与えていなかったが、マメヅタについては、光、水条件ともに良好な条件下でRGRが高くなる傾向があった。2種の着生植物の光と水条件に対する反応は、ホスト樹木内の着生部位の環境条件と概ね一致していた。比較的明るい環境である樹冠上部に生育するノキシノブの成長、生存には、光条件が重要な役割を果たしており、より湿度の高い樹幹部から樹冠中央部に分布が集中するマメヅタの成長には、光条件とともに水条件も重要である事が示唆された。

キーワード：樹木内の垂直分布、成長速度、暖温帯林、着生シダ、光条件、水供給

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