Research paper

Response of two epiphyte species to nitrogen and phosphorus fertilization at a humid subtropical rainforest in northeastern Taiwan

Guan-Zhong Huang,[1]   Teng-Chiu Lin[1,2]

【 Summary 】

Several studies indicate that epiphytes share similar nutrient limitation with soil-rooted plants in the same ecosystem. Compared to trees, epiphytes have a much shorter life span so that epiphytes should respond more rapidly to fertilization than trees and can be used as an indicator for ecosystem nutrient limitation. We conducted a fertilization experiment on two epiphyte species *Haplopteris zosterifolia* and *Asplenium antiquum*, a basket-shaped epiphyte that collects litterfall and forms a nutrient rich substrate, at the Fushan Experimental Forest of northeastern Taiwan. The co-occurrence of the two species is common but they can also grow alone. We compared nutrient concentrations and nutrient ratios nine months after fertilization. The results show that adding the nutrients, nitrogen (N) or phosphorus (P), did not lead to a greater biomass increment compared to the control group for both species. P fertilization increased P concentration and decreased the N : P ratio in both species, while N fertilization increased the foliar N concentration and decreased the C : N ratio only in *A. antiquum*. The positive response to P fertilization but not N fertilization for both species fits the general assumption of greater P than N limitation at low elevation forests in Taiwan. The biomass change of *A. antiquum* over nine months was not different between individuals growing alone and individuals co-occurring with *H. zosterifolia*. In contrast, biomass of *H. zosterifolia* increased in co-occurring individuals but decreased in individuals growing alone possibly due to drought mitigation from the substrate of *A. antiquum*. In summary, our study suggests that epiphyte growth is probably more limited by water than by nutrients. Although high atmospheric nitrogen deposition at the Fushan Experimental Forest and elevated atmospheric CO_2 concentrations have the potential to enhance plant growth, the effects may not be realized for epiphytes if water supply is not increased. Our results also indicates that although nutrient limitation may be similar between epiphytes and trees, the ultimate limiting factor may be different because water shortage is less a problem for trees than epiphytes in moist forests.

Keywords: *Asplenium*, epiphyte, fertilization, Fushan, nutrient limitation.

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[1] Department of Life Science, National Taiwan Normal Univ., 88, Sec.4, Tingzhou Rd., Wenshan Dist., Taipei 11677, Taiwa. 國立臺灣師範大學生命科學系，11677台北市文山區汀州路4段88號。

[2] Corresponding author, e-mail:tclin@ntnu.edu.tw 通訊作者。

研究報告

施氮、磷肥對在臺灣東北部潮濕亞熱帶森林中
兩種附生植物的影響

黃冠中[1]　林登秋[1,2]

摘　要

有研究指出限制附生植物生長的營養因子與土生植物相同，而附生植物的生長週期較木本植物短，應更快反應施肥的效果而作為生態系營養限制因子的指標。本研究在福山試驗林對巢蕨與垂葉書帶蕨兩種附生植物進行施肥實驗，兩物種經常生長在一起但亦可獨自生長，而巢蕨籃狀的構造能攔截枯落物累積形成豐厚的基質。經九個月施氮或磷肥後，結果發現生物量在實驗組與控制組間並無顯著的差異，在營養方面施氮肥組中僅巢蕨葉片的含氮量顯著較高、碳氮比明顯較低，但施磷肥組則是兩種附生植物葉片含磷量皆顯著較高、氮磷比則顯著較低，符合臺灣低海拔森林普遍的營養限制為磷的預期。生長形式方面，獨自生長的巢蕨生物量不會受垂葉書帶蕨共生影響，但與巢蕨共同生長的垂葉書帶蕨或因基質而能減緩乾旱的影響，使生物量顯著高於獨自生長的個體。本研究顯示附生植物的生長主要受到水份的影響而非營養，雖然高氮沉降及二氧化碳濃度可能有助於植物生長，但在福山試驗林若水分的限制若未消除，對附生植物的影響可能有限。另外研究也指出附生植物與木本植物所缺乏的營養成分類似，但後者受水分的限制不如附生植物嚴重，因此兩者最主要的生長限制因子應有所差異。

關鍵詞：巢蕨、附生植物、施肥、福山、營養限制。

INTRODUCTION

Epiphytes are an important component of many moist tropical and subtropical forests, contributing up to 1/3 of the plant species in some forests (Kreft et al. 2004). Because epiphytes have much lower proportions of supporting tissues relative to photosynthetic tissues than woody plants, they have contribute more to forest nutrient capital than what their biomass represents (Hsu et al. 2002). Unlike woody plants, the roots of epiphytes do not grow into ground soils so that they acquire water and nutrients mostly, if not entirely, from atmospheric deposition (Andrade and Nobe 1997, Coxson and Nadkarni 1995). Through interception / uptake of water and nutrients

dissolved in it, epiphytes help retain water and nutrients within the ecosystem and thereby minimize surface runoff and nutrient leaching. Such water and nutrient retention may play an important role in forest hydrology and nutrient cycling, but very few studies have investigated the role of epiphytes in forest nutrient cycling (Nadkami 1984, Zotz et al. 2010).

Nutrient limitation is a salient topic in studies of ecosystem productivity and nutrient cycling. The most common limiting nutrient in temperate regions is nitrogen (N), whereas in humid tropics with old soils, phosphorus (P) is often more limiting than nitrogen (Vitousek 1984, Aber et al. 1989, Vitousek and

Howarth 1991). The most direct evidences of nutrient limitations came from fertilization experiments that compare plant growth in plots / forests with and without the addition of N and / or P, or other mineral elements (Mirmanto et al.1999). It usually takes at least 3-5 years to observe the effects of fertilization on tree growth. Studies in a Hawaiian forest reported that epiphytes share the same nutrient limitation with the soil-rooted plants (Vitousek and Turner 1995, Hobbie and Vitousek 2000, Benner and Vitousek 2007). If epiphytes share similar nutrient limitations with trees, then because, epiphytes have a much shorter life span compared to trees, their responses to fertilization is much more rapid and these plants should be good surrogates of ecosystem nutrient limitation.

In this study, we used a fertilization experiment to assess epiphyte nutrient limitation at the Fushan Experimental Forest of northeastern Taiwan. Although many soil scientists and ecologists believe that most low elevation forests in Taiwan are P-limited, currently there is no direct evidence from fertilization experiments on natural forests. If epiphytes indeed share the same nutrient limitation with soil-rooted plants, our results would provide empirical data for this fundamental question in forest ecology.

Two epiphyte species, *Asplenium antiquum* and *Haplopteris zosterifolia*, were used in the study. Each of the two epiphyte species can grow independently from the other, but their co-occurrence is common (Jian et al. 2013). The *Asplenium* is among the most common epiphyte groups in humid tropical and subtropical forests, including those in Taiwan (Fayle et al. 2009, Hsu et al. 2002, Jian et al. 2013). The leaves of *Asplenium* are radially arranged and form a basket-shaped structure, which enables them to collect water and canopy litterfall. The accumulated substrate is very rich in nitrogen and other nutri-

ent elements (Yang et al. 2001, Yen 2007) and is capable of holding water nearly 6 times its dry weight so this could be an important water source for both *Asplenium* and its co-occurring epiphytes (Jian et al. 2013).

It has been reported that *A. antiquum* facilitates the growth of *H. zosterifolia* through drought mitigation (Jian et al. 2013). Through nutrient analysis, the latter study found no evidence of nutrient enhancement from the substrate of *A. antiquum* to *H. zosterifolia* because foliar nutrient concentrations were not different between *H. zosterifolia* growing alone and growing under *A. antiquum* (Jian et al. 2013), however, considering that *H. zosterifolia* growing under *A. antiquum* had more and longer leaves (Jian et al. 2013), the effects of nutrient enhancement cannot be ruled out. If *A. antiquum* enhances nutrient availability for *H. zosterifolia*, then the response of *H. zosterifolia* to nutrient addition (fertilization) should be less prominent in *H. zosterifolia* co-occurring with *A. antiquum* than in those growing alone. On the other hand, if the fertilization effect is not different between the two growth types of *H. zosterifolia*, then the lack of a nutrient enhancement effect is supported. Based on the common notion that low elevation forests in Taiwan are P-limited, we hypothesized that, compared to N addition, P addition should have a greater positive effect on biomass and nutrient enhancement in the two epiphyte species (H_1). In addition, because the substrate of *A. antiquum* is rich in organic matter that might provide nutrients for the co-occurring *H. zosterifolia*, we expect fertilization to have a smaller positive effect on *H. zosterifolia* co-occurring with *A. antiquum* than those growing alone (H_2).

METHODS AND MATERIALS

The study was conducted at the Fushan

Experimental Forest, a subtropical rainforest in northeastern Taiwan (24°34″N, 121°34″E). The elevation of Fushan Experimental Forest varies from 400 to 1400 m, and the mean annual precipitation is 4240 mm (Lin et al. 2011). Relative humidity is more than 90% throughout the year (Hsu et al. 2002, Hsia and Hwong 1999). The Fushan Experimental Forest is very rich in epiphytes, particularly along streamsides with a total of 65 vascular epiphyte species belonging to 20 families (Taiwan Forestry Research Institute 1989). We located 24 *A. antiquum* that grew independently from other epiphytes, 24 that co-occurred with *H. zosterifolia*, and 30 *H. zosterifolia* that grew independently. We divided these plants into three treatments: adding nitrogen (+N), adding phosphorus (+P) and control. Each month, we added 3 g urea for +N treatment to the epiphytes and 3 g $Ca(H_2PO_4)_2$ for +P treatment. The fertilizers were dissolved in 15 g of water and we added 15 g of water for the control treatment per month. However, for the +P treatment after the first 3 months we changed to 2.26 g Na_2HPO_4 per month due to low solubility of $Ca(H_2PO_4)_2$ (Aerts et al. 1992, Campo and Carlos 2004, Mirmanto 1999, Wanek and Zotz 2011). The total amount of N fertilizer we added was 24 g urea for +N treatment and P fertilizer was 9 g $Ca(H_2PO_4)_2$ and 11.3 g Na_2HPO_4 for +P

treatment. Based on our field measurements of the mean crown area of the two epiphytes of one m^2, the annual fertilization addition was approximately 166 kg ha^{-1} yr^{-1} for N and 65 kg ha^{-1} yr^{-1} for P. To avoid the washing away of fertilizers by rains, we installed a dripping bottle on each plant. We tested the dripping rate prior to the experiment to assure that the solution was gradually added to the plant in 30 days. During the experimental period, however, some of the plants were lost or damaged due to wind or animal disturbance. The initial and final number of plants in each treatment are listed in Table 1.

To exam the effects of fertilization, we measured the number of leaves and the length of 5 randomly selected leaves of each plant. Then we randomly took one leaf of *A. antiquum* and 3-5 leaves of *H. zosterifolia* back to the laboratory, where they were dried at 45℃ for a week and then weighed. We used the weight-length ratio of the sampled leaves to estimate the biomass of each plant. For each foliar sample, the concentration of C and N was analyzed using a CHNOS Elemental Analyzer (Elementar vario EL III, Hanau, Germany) and P, K, Ca, and Mg using an Inductively coupled plasma atomic emission spectrophotometer (ICP-AES) JY 2000 (Labcompare, South San Francisco, California, USA).

Table 1. Initial and final sample size of each of the three living forms of two epiphyte species: *Asplenium antiquum* growing alone, *Haplopteris zosterifolia* growing alone and co-occurrence of the two species. During the fertilization experiment period, some of the initial plants were lost or damaged due to wind or animal disturbance. +N: adding nitrogen, +P: adding phosphorus

Treatment	Epiphyte type					
	A. antiquum		*H. zosterifolia*		Co-occurring	
	initial	final	initial	final	initial	final
Control	8	7	10	7	8	8
+N	8	7	10	10	8	8
+P	8	8	10	9	8	8

We used general linear models to examine the effects of two independent variables, growth type (co-occurring and growing alone) and fertilization (+N, +P, and control), on biomass, nutrient contents, C:N ratio, and N:P ratio (dependent variable) using SPSS 22.0 (IBM Inc., Armonk, New York, USA). To account for variation among plants before the treatment, we used the post-treatment: pre-treatment ratios for all statistical analyses.

RESULTS

Differences between growth types

Post-treatment biomass of *A. antiquum* was greater than pre-treatment biomass (i.e., (post-treatment biomass)/(pre-treatment biomass) > 1) both in individuals co-occurring with *H. zosterifolia* (1.27±0.38) and in individuals growing alone (1.18±0.38); however, post-treatment biomass as a proportion of pre-treatment (hereafter all post-treatment values refer to the values as proportions of pre-treatment values) biomass was not significantly different between the two growth types (Table 2). In contrast, the post-treatment biomass of *H. zosterifolia* was greater in individuals co-occurring with *A. antiquum* (1.14±0.24) than individuals growing alone (0.79±0.29) (Table 2). Post-treatment concentrations of all analyzed elements and nutrient ratios (i.e., C:N and N:P ratios) were not different between the two growth types for the two species, except for potassium in *A. antiquum* (Table 3). In *A. antiquum*, the post-treatment potassium concentration was greater in the co-occurring individuals (0.94±0.13) than in individuals growing alone (0.74±0.14) (Table 2).

Differences among fertilization treatments

Post-treatment biomass was not significantly different among fertilization treatments for either epiphyte species but post-treatment concentrations and nutrient ratios were (Fig. 1, Fig. 2, Table 2). For *A. antiquum*, fertilization led to a greater concentration of the added nutrient. Post-treatment N concentration was greater in the +N group than in either the +P group or the control group, and plants in the

Table 2. Results of the general linear models of effects of fertilization (adding nitrogen, adding phosphorus, and control) and growth type (growing alone and co-occurring of *Asplenium antiquum* and *Haplopteris zosterifolia*) on biomass, concentrations of carbon, nitrogen, and phosphorus. None of the interaction effects are significant so they are not included. The values in the table are *F* statistics and *p* values

Response variable	Independent variable	*A. antiquum*		*H. zosterifolia*	
		F	*P*	*F*	*P*
Biomass	Growth type	0.87	0.36	23.5	< 0.001
	Fertilization	2.78	0.07	1.29	0.29
N	Growth type	0.99	0.33	0.19	0.66
	Fertilization	11.10	< 0.001	2.89	0.07
P	Growth type	0.659	0.42	0.68	0.42
	Fertilization	7.92	0.001	5.15	0.01
C:N	Growth type	2.06	0.16	0.77	0.39
	Fertilization	9.24	0.001	1.79	0.18
N:P	Growth type	0.02	0.89	0.22	0.64
	Fertilization	20.8	< 0.001	21.0	< 0.001

Table 3. Results of three general linear models of effects of fertilization (adding nitrogen, adding phosphorus, and control) and growth type (growing alone and co-occurring of *Asplenium antiquum* and *Haplopteris zosterifolia*) on concentrations of potassium, calcium, and magnesium. None of the interaction effecs are significant so they are not included. The values in the table are *F* statistics and *p* values

Response variable	Independent variable	A. antiquum		H. zosterifolia	
		F	P	F	P
K	Growth type	24.5	< 0.0001	< 0.001	0.98
	Fertilization	1.96	0.16	0.16	0.86
Ca	Growth type	0.66	0.42	< 0.001	0.99
	Fertilization	1.23	0.30	3.29	0.047
Mg	Growth type	0.21	0.65	0.15	0.70
	Fertilization	2.96	0.06	2.99	0.061

latter two treatments had similar concentrations (Fig. 1). In contrast, the post-treatment C:N ratio was smaller in the +N group than in the other two groups that were not different from each other (Fig. 1). Similarly, the +P group had a greater post-treatment P concentration than the other two groups, which were not different from each other (Fig. 1). The +N group had a higher post-treatment N:P ratio than the control group which was greater than the +P group (Fig. 1). For *H. zosterifolia*, adding P had a positive effect on P concentration but adding N had no significant effect on N concentration and C:N ratio (Fig. 2). The +P group had a greater post-treatment concentration of P than did the other two groups, which were not different from each other. The +P group had a smaller N:P ratio than the control group, which was smaller than the +N group (Fig. 2). For both species, fertilization had no effect on the concentrations of all elements that were not included in the fertilizers, except calcium in *H. zosterifolia*. In *H. zosterifolia*, the post-treatment calcium concentration was greater in the + P group (1.07 ± 0.27) than in the +N group (0.86 ± 0.24), while the control group (0.95 ± 0.18) was not different from either the +N or +P group (Fig. 1 and Fig. 2, Table 3).

DISCUSSION

The lack of response to N or P fertilization suggests that growth of the two epiphytes and maybe many other epiphytes at the Fushan Experimental Forest is probably not nutrient limited. A study at the Fushan Experimental Forest proposed that *A. antiquum* facilitates the growth of *H. zosterifolia* through drought mitigation (Jian et al. 2013). This facilitation effect is supported by our result of greater biomass increment in *H. zosterifolia* co-occurring with *A. antiquum* than growing alone. Possibly, at the Fushan Experimental Forest and many other tropical and subtropical forests, epiphyte growth is more limited by water than by nutrients. Although the Fushan Experimental Forest has more than 200 rainy days annually and a mean annual rainfall of 4240 mm (Lin et al. 2011), periods of mini-drought are not uncommon (Martin et al. 2010). During our 9-month study (October 2014-June 2015), there were 7 mini-drought periods with at least 5 consecutive rainless days with a maximum of 8 days (Fig. 3). Although during such rainless periods, soil moisture may remain high and soil-rooted plants were largely unaffected, epiphytes were probably affected due to the lack of access to
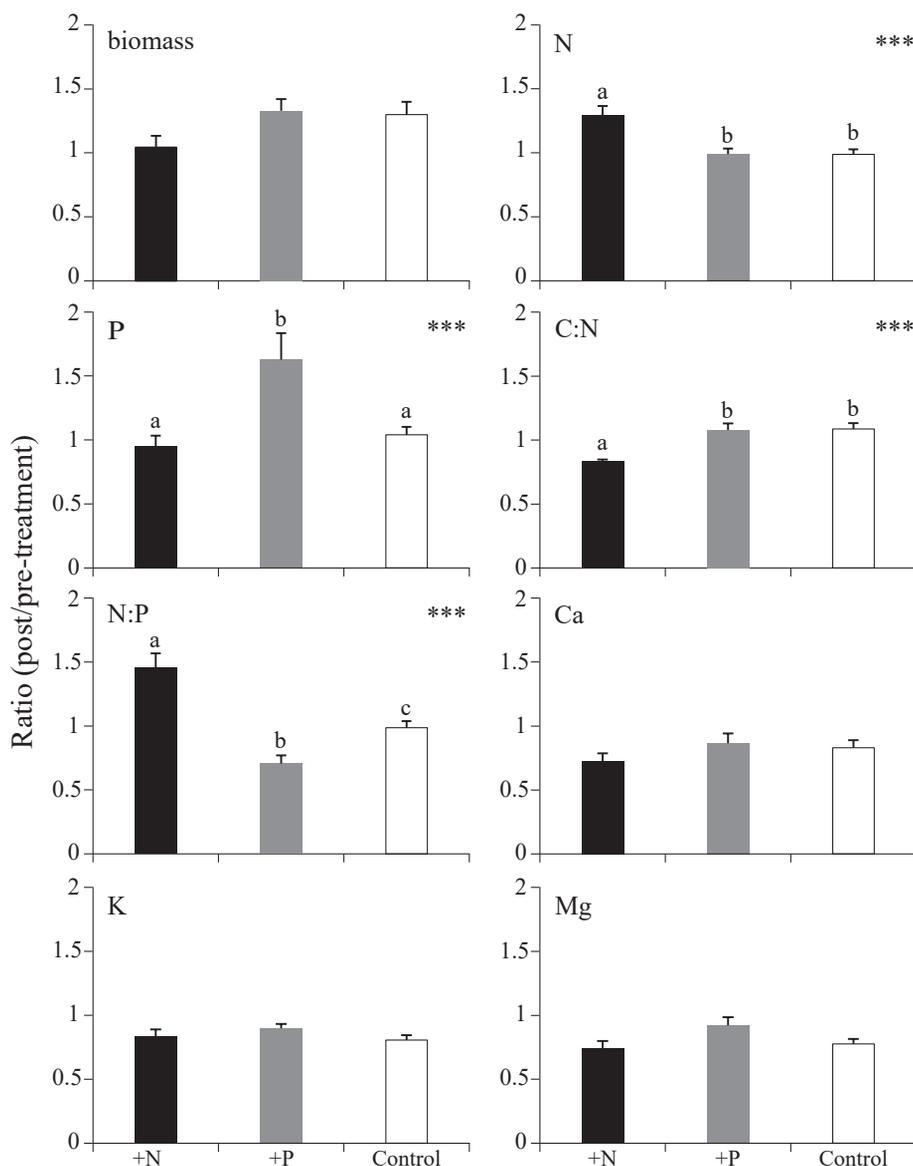
Fig. 1. The effects of fertilization treatment (+P: adding phosphorus, +N: adding nitrogen) on biomass, foliar nutrient concentrations, and nutrient ratios of *Asplenium antiquum*. The result was expressed as the ratio of post-treatment/pre-treatment such that a ratio > 1 indicates an increase in biomass or nutrient concentration and a ratio < 1 means decreases in biomass or nutrient concentration. For nutrient ratio, the ratio change indicates changes in relative abundance of the two elements. Error bar: 1 standard error. *, ** and * statistically significant among treatments at α = 0.05, 0.01 and 0.001 levels, respectively. Bars with different letters are significantly different at α = 0.05 based on Tukey's post-hoc tests.**
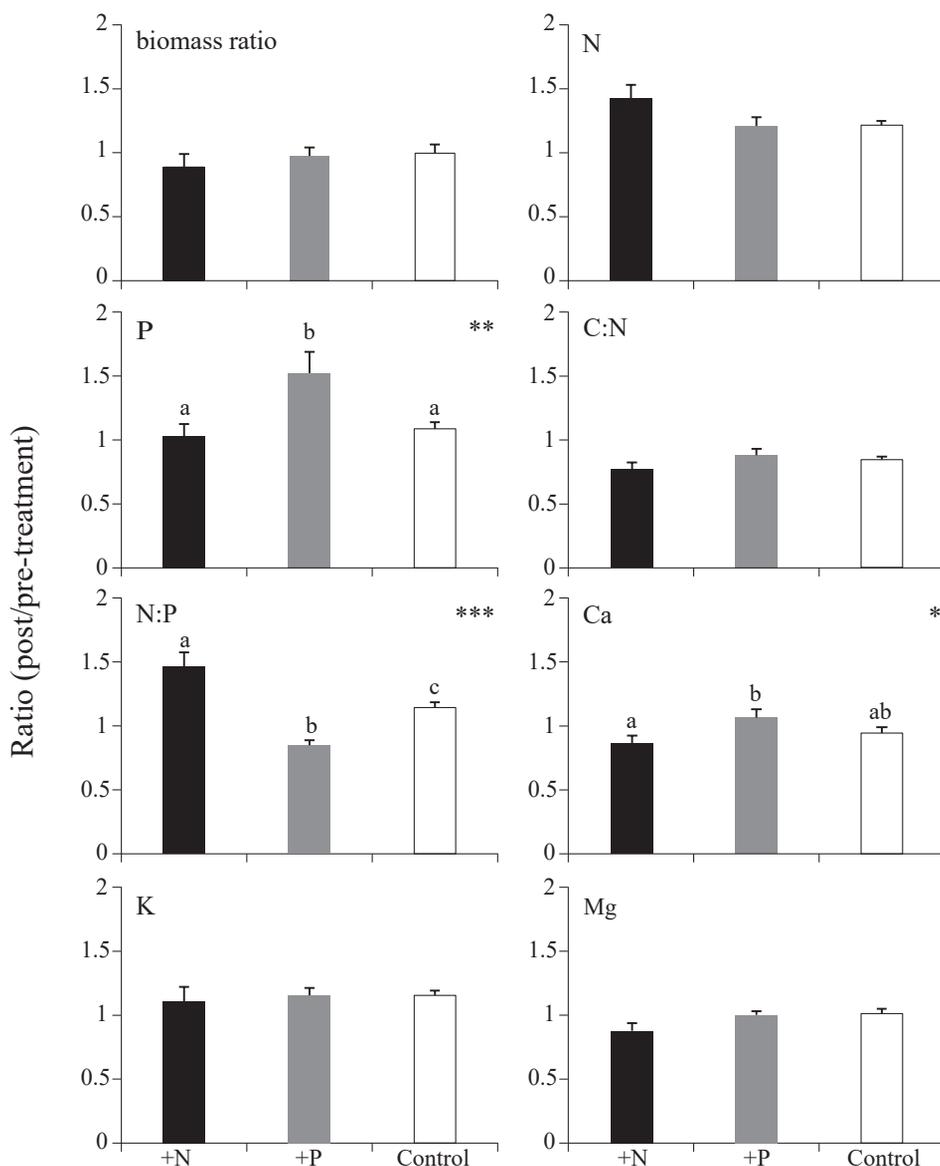
Fig. 2. **The effect of fertilization treatment (+P: adding phosphorus, +N: adding nitrogen) on biomass, foliar nutrient concentrations, and nutrient ratio of *Haplopteris zosterifolia*. The results are expressed as the ratio of post-treatment / pre-treatment such that a ratio > 1 indicates an increase in biomass or nutrient concentration and a ratio < 1 means decreases in biomass or nutrient concentration. For nutrient ratio, the ratio change indicates changes in relative abundance of the two elements. Error bar: 1 standard error. *, ** and *** statistically significant among treatments at α = 0.05, 0.01 and 0.001 levels, respectively. Bars with different letters are significantly different at alpha (α)= 0.05 based on Tukey's post-hoc tests.**

soil water. Because fertilization did not lead to greater biomass increases, it is not surprising that the concentrations of K, Ca, and Mg were mostly unaffected.

Both increases in atmosphere CO_2 concentration and high atmospheric deposition of nutrient elements, especially N, have the potential to improve plant growth (i.e., by fixing more CO_2) and through which form a negative feedback to mitigate the warming trend (Veteli et al. 2002). Our results, however, indicates that such growth enhancement may not be observed among epiphytes if rainfall (frequency) does not increase. Because in humid forests, mini-droughts only (or mainly) affects epiphytes, our results also highlights the possibility that although nutrient limitation may be similar between soil-rooted plants and epiphytes, as suggested by several studies in Hawaii (Benner and Vitousek 2007), the ultimate limiting factor for their growth may be different. The difference in the ultimate limiting factor implies that the use of epiphytes as a surrogate of ecosystem

nutrient limitation has limits. It is worth noting that over the last 30 years, the total rainfall and frequency of small rainfall events has increased at the Fushan Experimental Forest (Chang C.T. unpublished data). If this trend continues, and the water constraint is eased, the effects of fertilization on epiphytes may then be observed.

Although adding nutrients did not lead to a greater increase in biomass, it did increase the concentrations of the added nutrient and the associated nutrient ratios. In other words, fertilization affected plant nutrient composition, although such an effect did not lead to growth enhancement. Both nutrient concentrations and nutrient ratios (e.g., C:N, N:P) are important factors affecting litter decomposition. Thus, although fertilization had no observable effect on epiphyte growth, it could affect nutrient release through decomposition and therefore nutrient availability in the system (Nadkarni 1984). Once the nutrients are released, however, which mostly takes place on the forest floor, it is the soil-rooted plants,
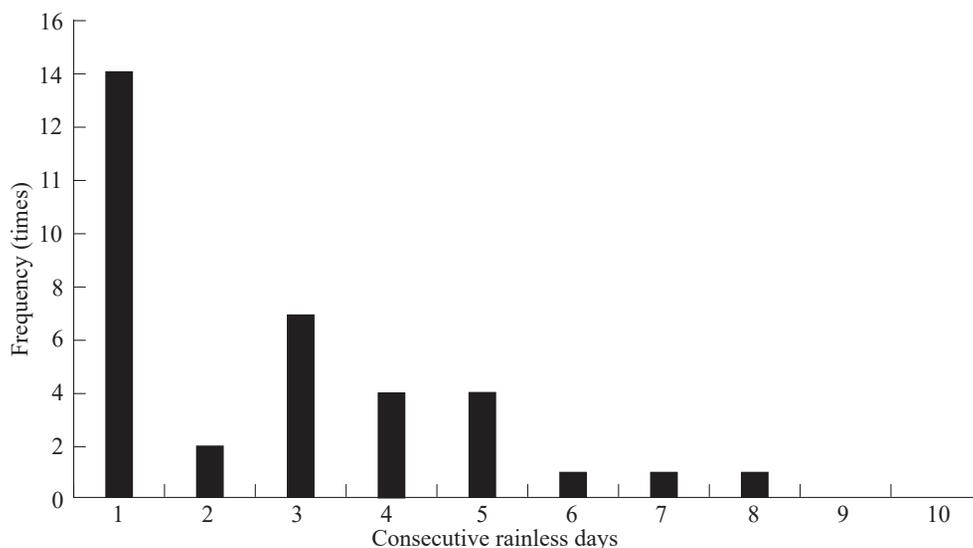
Fig. 3. Frequency distribution of rainless period of at least 1 days between October 2014 and June 2015 at the Fushan Experimental Forest (Shuanglianpi station, Central Weather Bureau).

not epiphytes themselves, that are more directly affected.

Notably, adding N and P, respectively, led to increases in N and P concentrations for *A. antiquum*, however, for *H. zosterifolia*, adding P also led to increases in P concentration, but adding N had no effect on N concentration. We do not have data allowing us to propose any explanation for this finding, but it does fit the general assumption of greater P than N limitation for low-elevation ecosystems in Taiwan. Maybe the very high N deposition, 26 kg ha^{-1} yr^{-1} (Lin et al. 1999), at the Fushan Experimental Forest is more than enough to meet the growth demand of epiphytes that typically have low nutrient concentrations (Mitchell et al. 2004). Thus, before water and phosphorus demands are satisfied, adding N has little effect on foliar N concentration.

One limitation of our study is the lack of a treatment with both N and P addition due to the difficulty in finding enough plants in accessible locations (many of the epiphytes are located too high in the tree canopies). Thus, although the growth of epiphytes may be water limited, the possibility of co-limitation by both N and P as suggested for some ecosystems (Craine et al. 2008, Wright et al. 2011) cannot be ruled out. Using epiphytes that are more easily accessible (e.g., those growing on low parts of the host trees) would be a good way to comprehensively examine nutrient limitation of epiphytes.

CONCLUDING REMARKS

Our canopy fertilization had no observable effects on epiphyte biomass; however, P fertilization increased P concentration and decreased N:P ratio in the two experimental epiphyte species, but N fertilization increased the foliar N concentration and decreased C:N

ratio in only one species, *A. antiquum*. These results support a greater P than N limitation at the Fushan Experimental Forest as well as the general assumption of greater P than N limitation in low elevation forests in Taiwan. Biomass changes of *A. antiquum* over the study period were not different between individuals growing alone and individuals co-occurring with *H. zosterifolia*, however, the biomass of *H. zosterifolia* increased in co-occurring individuals but decreased in individuals growing alone, possibly due to drought mitigation from the substrate of *A. antiquum* proposed in a previous study. Our results indicate that although nutrient limitation may be similar between soil-rooted plants and epiphytes at the Fushan Experimental Forest, the ultimate limiting factor could be different because water shortage is unlikely a problem for trees in such forests

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