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ORIGINAL ARTICLE

Nitrogen fixation of epiphytic plants enwrapping trees in Ailao Mountain cloud forests, Yunnan, China

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Abstract Epiphytic plants play an important role in the nutrient cycle of forest ecosystems. There had been fewer studies in subtropical regions than in other climate zones. Prior research showed that the canopy epiphyte could fix nitrogen combined with microorganism in tropical forest. The epiphytic plants enwrapping trees in canopy layer are very abundant in the subtropical mountainous cloud forest of Ailao Mountain (central and southern Yunnan Province, SW China). This forest lacks widespread nitrogen-fixing plants, and the nitrogen origin is elusive. Maybe there also exist such nitrogen-fixing systems in epiphyte community. Nitrogen-fixing potentials of canopy epiphytes increased greatly from dry season to wet season. There occurred an obvious difference on the epiphytic nitrogen fixation abilities between upper canopy layer and sub-canopy layer in alternant period between wet season and dry season. Epiphytic nitrogen-fixing potentials for the subtropical moist forest in Ailao Mountains ranged between 0.027 and 2.24 kg ha^{-1} $year^{-1}$. Our results indicate that the canopy epiphytes in the subtropical moist forest of Ailao Mountains can fix a significant amount of atmospheric nitrogen. This finding suggests a new nitrogen source for the subtropical forest ecosystem, thus can have profound impact on the studies of nitrogen cycling.

Keywords Epiphytic plants · Subtropical forest · Nitrogen fixation · Ailao Mountain · China

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Introduction

Epiphytic plants play important roles in sustaining biodiversity, facilitating water and nutrient cycling in mountainous forests (Lowman 2001; Nadkarni et al. 2001). There had reports that lichen and moss communities could fix nitrogen gas from the atmosphere (Bentley and Carpenter 1984; Yatazawa 1983). Further works were carried out in tropical forests (Kai et al. 2003; Reed et al. 2008).

The epiphytic plants enwrapping trees in canopy layer are very abundant in temperate and tropical forests in China (Wu 1987). Little work had been carried out to investigate the role of epiphytic plants in the subtropical mountainous forests, especially in China (Liu et al. 2008; Xu and Liu 2005; Xu et al. 2006).

Epiphytic plants usually could not fix nitrogen by themselves but by a combination with microorganisms (Bentley and Carpenter 1984). We supposed that there also existed nitrogen-fixing systems consisting of epiphytes and microorganisms. We collected epiphytic samples with similar ways of biodiversity research and hoped that we could get epiphytic species as many as possible by species identification. By observing the accumulation of C_2H_4 by acetylene reduction method, our aims were to determine whether the ability of fixing nitrogen from the atmosphere widely existed in epiphytic community and quantify it in a typical subtropical mountainous forest in China. Lastly, we also determine the nitrogen contents of epiphytic samples to quantify their contribution to nutrient storage as their plentiful biomass.

Materials and method

The natural vegetation of subtropical mountainous (2,000–2,600 m), central and southern Yunnan Province, SW China consists of evergreen, broad-leaved forest (Takawa 1997; Wu 1987). Species of oak and chestnut (Fagaceae) tend to dominate those forests. Only those areas with relatively poor access have remained as natural ecosystems, relatively undisturbed by human influences. Ailao Mountain National Nature Reserve (NNR) of 504 km^2 was believed to be the largest tract of natural broad-leaved forest in China, with a great number of epiphytic plants enwrapping trees in the stems and branches. About 85% of the annual rainfall comes from the wet season from May to October (Qiu et al. 1998; Young and Wang 1989). The height of the forest is about 20–25 m.

Xishuangbanna Tropical Botanical Garden has a Forest Ecosystem Research Station (FERS) at Xujiaba (24°32′ N, 101°01′ E; 2,400–2,600 m) immediately adjacent to a 5,100-ha area of Ailao Mountain NNR. We chose a test plot about 1 ha nearby FERS.

Xu and Liu (2005) had reported that epiphytic plants enwrapping trees in canopy layer were always composed of moss, ferns, little lichen and spermatophyte, and little humus such as dead bodies of plants and animals in Ailao Mountain Forest. About 80% of the total biomass was coming from moss and fern. In our sampling trees, lichens were few and almost all occurred over the height of 15 m. Here, we did not collect lichens and removed spermatophyte and humus carefully as much as we could. We collected epiphytic samples with 20×20-cm scale as Xu and Liu (2005) mostly used.

At the beginning, we need to determine whether the nitrogen fixation ability is widely existent in the epiphytic community. Our samples were mixed by many kinds of epiphytic plants and the epiphyte covered almost all kinds of host tree, so we need to make sure that the nitrogen fixation ability still existed while the constitutions and host trees were varied. We made two experiments on species and proportion variation in dry season and selected six kinds of host trees to determine.

Then, we need to quantify nitrogen fixation by the canopy epiphytes from the atmosphere. We collected the mixed samples to accord with the natural living conditions as much as possible; furthermore, we regarded the epiphyte and microorganism as a whole to determine the nitrogen-fixing ability. We collected samples in the dominant tree species.

Species and proportion variation

First, we collected four moss species, which were *Bazzania albifolia* Horik, *Bazzania oshimensis* (Steph) Horik, *Plagiochila nepalensis* (Spreng) Lehm. & Lindenb, and *Plagiochila fruticosa* Mitt. They were all dominant species in our plot and in Xu and Liu's (2005) report.

We made two treatments for every species. The first treatment was that the sample just consisted of one of the four original species. The other treatment was that we added one or two different species and put them together according to average coverage. The original and later added species were shown as Table 1. The scale of every sample was about 20×20 cm, and the fresh weight was about 5–10 g. We obtained 12 samples.

Second, we select one of the four dominant species and got five samples. One sample just consisted of *B. oshimensis* (Steph) Horik and others included other kinds of species besides it. The total amount of species and the proportion of *B. oshimensis* (Steph) Horik in every sample were shown as Table 2. The scale of every sample remained the same as in the first experiment.

All samples were collected in the dry season (March 2006) to avoid rainfall impact on the nitrogen fixation ability of epiphytic plants (Jani et al. 2005).

Variation of host tree

We would determine whether the nitrogen fixation ability of epiphytic plant exists widely in most host trees. We chose 24 and six kinds of host trees (the DBH must be over 30 cm), which were *Lithocarpus xylocarpus*, *Castanopsis wattii*, *Lithocarpus chintungensis*, *Schima noronhae*, *Hartia sinensis*, and *Manglietia insignis* in December 2006, and they were all dominant tree species in Ailao Mountain Forest.

We obtained samples at 0-, 1.3-, and 1.5-m height on the stems in sub-canopy layer by a reseau of about 20×20-cm scale. We mixed the collected samples from the same tree and got 24 samples to represent every host tree.

Quantifying nitrogen fixation in epiphytic plants

Xu and Liu (2005) found that almost all epiphytic species in Ailao Mountain Forest could be found when the amount

Table 1 Single species and mixed species

Original species	Added species to comparison samples	
Bazzania albifolia Horik	1	No
	2	*Syrrhopodon gardneri* (Hook) Schwaegr
	3	*Papillaria feae* Fleisch
		Hymenophyllum
Bazzania oshimensis (Steph) Horik	1	No
	2	*Trachypus humilis* Lindb
	3	Two kinds of Pteridophyta
Plagiochila nepalensis (Spreng) Lehm. & Lindenb	1	No
	2	*Homaliodendron scalpellifolium* (Mitt) Fleisch
	3	*Lejeunea curviloba* Steph
		Horikawaea nitida Nog
Plagiochila fruticosa Mitt	1	No
	2	Hymenophyllum
	3	*Dicranum scoparium* Hedw
		Homaliodendron scalpellifolium (Mitt) Fleisch

of host trees (the DBH must be over 30 cm) reached eight, and they also reported that the distributions of epiphytic species were different in different heights in this forest.

To reduce the interval and finish the epiphytic collection quickly, we randomly chose 16 and two kinds of host trees (DBH over 30 cm) to collect epiphytic samples in November 2005 and in January, February, March, June, and October 2006. We hoped that we could collect most epiphytic species and quantify their ability as a whole to present the epiphytic community in Ailao Mountain Forest.

One tree species of these 16 trees was *L. chintungensis*, which was the dominant tree species in arboreal layer, and the other tree species was *Vaccinium duclouxii*, which was the dominant tree species in the sub-arboreal layer. They were dominant species not only in our plot but also in the whole forest.

Methods of collecting epiphytic plants were similar with the gathering ways of biodiversity research to get species as many as possible (Cao and Guo 2000; Vellak and Paal 1999). In every tree, we obtained samples in two layers at different height. The height of sub-canopy layer was form 0 to 5 m, and the height of the upper canopy layer was about 10–15 m.

We obtained samples at 0-, 1.3-, and 1.5-m height on the stems in the sub-canopy layer by a reseau of about 20×20-cm scale. In the upper canopy layer, we began collecting epiphytic samples when the main branches occurred and got samples with 20×20-cm scales on the main branches. We would keep climbing until the tree could not afford. We selected new branches and collected samples of them with reseaus of about 10×10- or 5×20-cm scales every 2 m (Fig. 1). Then, we mixed the epiphytic plants in the same layer and chose a 20×20-cm scale to represent their layer. Lastly, we obtained 32 samples and waited for determination after every collection.

Acetylene reduction method

All the samples were sent to the laboratory quickly after collection and put into 300-ml culture bottles after

Table 2 Species amounts and proportion of *B. oshimensis* (Steph.) Horik. in different samples

Groups	Species	Species amount	Proportion (%)
1	*Bazzania oshimensis* (Steph) Horik	1	100
2	*Bazzania oshimensis* (Steph) Horik	3	85
	Two kinds of *Pteridophyta*		15
3	*Bazzania oshimensis* (Steph) Horik	2	70
	One kind of *Pteridophyta*		30
4	*Bazzania oshimensis* (Steph) Horik	2	65
	Hymenophyllum		35
5	*Bazzania oshimensis* (Steph) Horik	3	45
	Hyophila rosea Williams		25
	Brotherella henonii (Duby) Fleisch		30

Fig. 1 One colleague of our study group was operating at about 10- to 15-m height in a sampling tree

removing as much soil and humus as possible from the samples. We followed the acetylene reduction method to determine the ability of fixing nitrogen from the atmosphere (Deluca et al. 2004). Gas samples withdrawn from the tubes were analyzed for acetylene and ethylene with a Hewlett Packard 6890 gas chromatograph equipped with a flame ionization detector and Porapak T column.

Rates of C_2H_2 reduction were calculated as the rates of C_2H_4 production in the bottles over time. We used the unit milliliter C_2H_4 per gram per hour to record the nitrogen fixation activity. We used the ratio of C_2H_4/N_2 as 3:1.

Species identification and nitrogen content determination

After the process of determination of C_2H_4 production rates, we identified the moss species in the samples collected in March 2006 and then determined the nitrogen contents of these samples by Kjeldahl method.

Results

Nitrogen-fixing abilities in the entire samples collected for constitution and host tree varying experiment were determined by the accumulations of C_2H_4.

For the first species and proportion variation experiment, we analyzed the differences on C_2H_4 production rates of all samples with a two-way analysis of variance. There had been no difference on the C_2H_4 production rates whether the samples were just composed of the original single species or mixed multiple species.

For the second species and proportion variation experiment, we found the C_2H_4 accumulations not only in the samples only consisting of *B. oshimensis* (Steph) Horik but also in the mixed ones. At the same time, C_2H_4 production rates did not decline, although the proportions of *B. oshimensis* (Steph) Horik were reducing, but remained at a close level among these mixed groups (Fig. 2). The relation between the amounts of species, proportions of *B. oshimensis* (Steph) Horik, and C_2H_4 production rates was not obvious according to the results of the correlation coefficient.

C_2H_4 accumulations were found in all of the samples in the six kinds of host trees (Fig. 3). Variations of C_2H_4 production rates among different kinds of host trees were not significant.

We identified the moss species of samples in two height layers from the 16 host trees collected in March 2006. Species identification results showed that included are 29 genuses and 39 species of moss (Table 3). The average content of nitrogen in samples collected in March 2006 was 1.81% in the sub-canopy layer and 1.82% in the upper layer. The average N content of samples in the two layers was calculated as 1.82%.

Whether it was from the upper canopy layer or the sub-canopy layer, C_2H_4 accumulations were found in all of the samples of six times of quantifying collections from November 2005 to October 2006, except the samples collected in January 2006 which looked like air-dried and the nitrogen fixation activities were too low to be determined by gas chromatograph. There also had been no obvious difference on C_2H_4 production rates of epiphytic samples in different layers or different host trees,

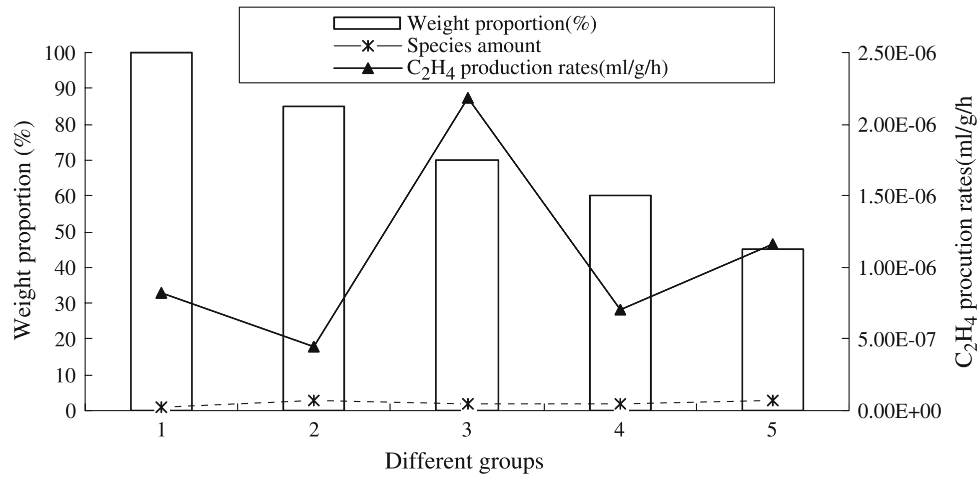

Fig. 2 C_2H_4 production rates of samples with different proportions of *B. oshimensis* (Steph.) Horik

except that there had been an obvious difference on C_2H_4 production rates of epiphytic samples in different layers collected in November 2005 and October 2006.

The average C_2H_4 production rate of epiphytic samples in the upper canopy layer and the sub-canopy layer is shown as Fig. 4.

There was a drought in January and February 2006, and the rainfall amount was close to zero in January and 2.4 mm in February. The date of samples in two layers declined close to zero, and the gas chromatograph could not determine the accumulation of C_2H_4 from November 2005 to January 2006. The average C_2H_4 production rates in both layers climbed to the level of 10^{-8}ml $g^{-1}h^{-1}$ in February with the 2.4-mm rainfall, then increased quickly to the level of 10^{-6}ml $g^{-1}h^{-1}$ in March with the rainfall amount increasing to 23.8 mm. After the dry season, the average rates of samples collected in June increased about 20 times than in March in both layers. At the end of the wet season, the average rate in October declined to about 10% of the rates in June in the upper canopy layer, but increased about twice in the sub-canopy layer.

Discussion

In the 32 samples collected in two canopy layers in March 2006, the amount of 29 genuses and 39 species of moss was more than the results from Xu and Liu (2005) who reported 24 genuses and 37 species of moss. So our collections could include most epiphytic species living in this area.

We found 22 genuses and 27 species in the upper canopy layer and 14 genuses and 18 species in the sub-canopy layer. Seven genuses and six species occurred in both layers. There lived more species in the upper canopy layer than in the sub-canopy layer. By collecting samples in different heights of layer in 16 host trees (DBH >30 cm), we had obtained as many species of epiphytic plants enwrapping trees in this forest as possible.

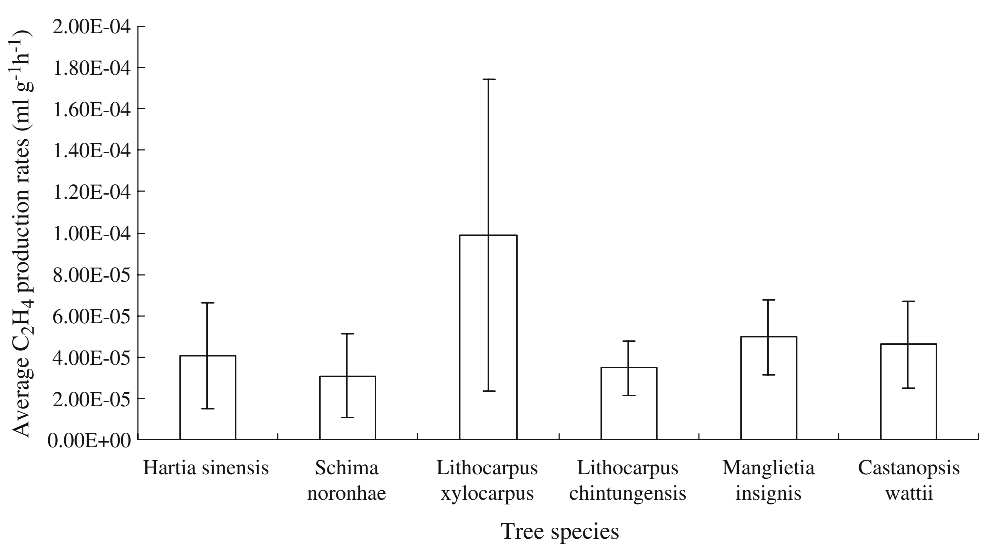

Fig. 3 Average C_2H_4 production rates of epiphytic plants in six kinds of dominant trees in Ailao Mountain Forest

Table 3 Species of moss in two layers

Species of moss in upper canopy layer	Species of moss in sub-canopy layer
Bazzania oshimensis (Steph) Horik	*Bazzania albifolia* Horik
Brotherella falcata (Dozy & Molk.) Fleisch.	*Bazzania oshimensis* (Steph) Horik
Clastobryella tenella Fleisch	*Brotherella henonii* (Duby) Fleisch
Dicranum scoparium Hedw	*Calyptothecium philippinense* Broth
Duthiella formosana Nog	*Calyptrochaea romasa* (Fleisch) B. C. Tan & H. Robins subsp. *spinosa* (Nog) B. C. Tan & P. J. Lin
Herbertus javanicus (Steph) Mill	*Cyrto-hypnum fusctum* (Besch) Wu, Crosby & He
Herbertus ramosus (Steph) Mill	*Eurhynchium eustegium* (Besch) Dix
Homaliodendron scalpellifolium (Mitt) Fleisch	*Fissidens nobilis* Griff
Horikawaea nitida Nog	*Homaliodendron flabellate* (Sm.) Fleish
Lejeunea curviloba Steph	*Homaliodendron montagneanum* (C. Muell) Fleisch
Meteoriella soluta (Mitt) Okam	*Homaliodendron scalpellifolium* (Mitt) Fleisch
Neckera yunnanensis Enroth	*Hyophila rosea* Williams
Neckeropsis calcicola Nog	*Neckeropsis crinita* (Griff) Fleisch
Papillaria feae Fleisch	*Plagiochila fruticosa* Mitt
Plagiochila fruticosa Mitt	*Plagiochila nepalensis* (Spreng) Lehm. & Lindenb
Plagiochila nepalensis (Spreng) Lehm. & Lindenb	*Ptychanthus striatus* (Lehm & Lindenb) Nees
Plagiochila ovalifolia Mitt	*Syrrhopodon gardneri* (Hook) Schwaegr
Plagiochila secretifolia Mitt	*Thuidium cymbifolium* (Dozy & Molk) Dozy & Molk
Plagiochila trabeculata Steph	–
Ptychanthus striatus (Lehm & Lindenb) Nees	–
Sematophyllum phoeniceum (C. Muell) Fleisch	–
Symphyodon perrottetii Mont	–
Thuidium cymbifolium (Doz & Molk) Doz. & Molk	–
Thuidium pristocalyx (C Muell) Jaeg	–
Trachypus humilis Lindb	–
Trismegistia undulata (Broth & Yas)	–
Wijkia deflexifolia (Ren & Card) Crum	–

– There had no any other moss species in the sub-canopy layer

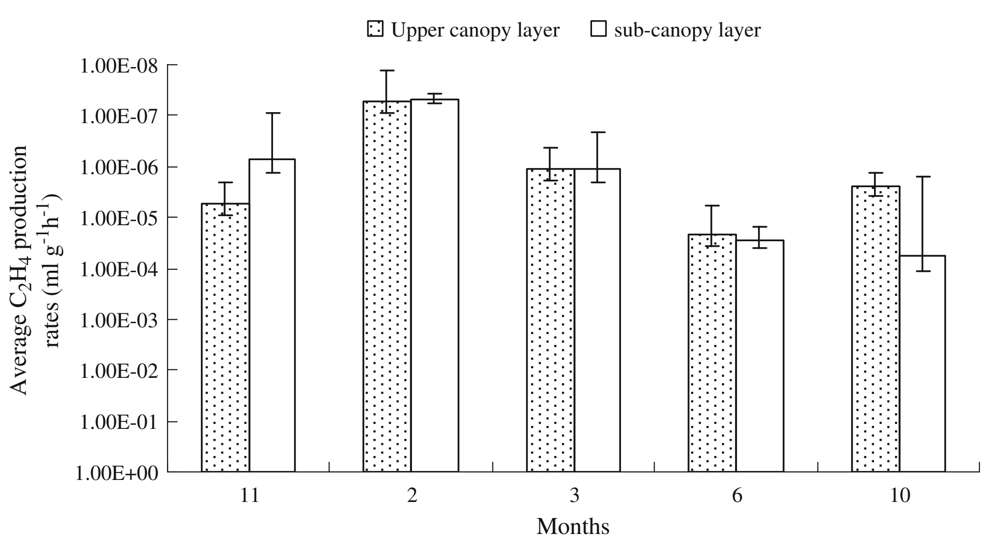

Fig. 4 Average rates of C_2H_4 production in two canopy layers of samples (November 2005–October 2006). The data varied greatly among different months, and we used the logarithmic scale in *Y*-axis

C_2H_4 accumulations were found in all of these 32 samples. We also found eight samples just consisting of one moss species. They were *B. albifolia* Horik, *B. oshimensis* (Steph.) Horik, *P. nepalensis* (Spreng) Lehm. & Lindenb, *P. fruticosa* Mitt, *Calyptothecium philippinense* Broth, *Thuidium cymbifolium* (Dozy & Molk..) Dozy & Molk, *Homaliodendron scalpellifolium* (Mitt.) Fleisch, and *Clastobryella tenella* Fleisch.

Brown (1982) reported that the symbiosis system between blue-green fungus and epiphytes was popular, and there also had been reports that the microorganism living in the epiphytes had the ability to fix nitrogen (Cabrerizo et al. 2001; Marko et al. 2002; Palmqvist et al. 1998). The nitrogen fixation ability was not closely related to the changes of epiphytic species amounts and proportions. There also had been no obvious difference on the abilities of samples collected in six kinds of host trees. The nitrogen fixation abilities widely existed in epiphytic plants enwrapping trees. This is because moss or other epiphytic plants could not fix nitrogen from the atmosphere by themselves but by combining with algae or other microorganisms, such as blue-green algae, and combining with lichen (Bentley and Carpenter 1984; Yatazawa 1983) and Nostoc hidden in moss leaves(Deluca et al. 2004). Maybe there also existed a nitrogen fixation symbiosis system within the epiphytic plants enwrapping trees in Ailao Mountain Forest.

The nitrogen fixation ability of epiphytic samples in dry season was very much lower than in wet season. The average C_2H_4 production rate of samples in the upper canopy layer in wet season was about ten times higher than in dry season, and the average rate of samples in the sub-canopy layer was about 100 times higher in wet season than in dry season. The rainfall was 49.6 mm in November and 50.4 mm in December 2005, but there had no rain in January 2006 and 2.4 mm in February. Compared with the obvious change of humidity, the temperature just varied from 9.3°C in November 2005 to 6.9°C in January 2006 and 8.9°C in February, but the C_2H_4 production rates declined from the level of about 10^{-6}ml $g^{-1}h^{-1}$ to the verge of zero in January and 10^{-8}ml $g^{-1}h^{-1}$ in February. With the amount of rainfall keeping on increasing, the increasing humility raised the water content of epiphytic plants, then the water stimulated the plants and improved the nitrogen fixation ability, and the C_2H_4 production rates could be determined again and increased quickly to hundreds and even 1,000 times higher.

But the long-term wetness may lead to the decline of epiphytic nitrogen fixation ability (Belnap 2002; Mullmeaux et al. 1983). In October 2006, the average C_2H_4 production rate of samples in the upper canopy layer stopped increasing, but declined about ten times more than in June 2006, and the difference on C_2H_4 production rates of epiphytic samples between different layers occurred again.

The variations of C_2H_4 production rates of samples between two canopy layers were significant only in November 2005 and October 2006, which were alternant periods between wet season and dry season. In November 2005, the average rate of samples collected in the upper canopy layer was about ten times higher than the ones collected in the sub-canopy layer. But in October 2006, the average rate of samples in the upper canopy layer just took 10% of the rate in the sub-canopy layer. Maybe the different living environments of different layers such as humidity factor could affect the nitrogen fixation ability of epiphytic plants. Gong et al. (2008) had reported that throughfall and stemflow could only be recorded when precipitation was over 3.7 mm in this forest, so the epiphytic plants living in the upper layer could touch rainwater earlier and intercept most part of rainfall especially with the wet season being over and the dry season beginning. But in wet season with long-term rainfall, the inter-space was more open in the sub-canopy layer which could help epiphyte alleviate the humidity affection.

Epiphyte is a kind of organism changed by water, and water can affect the nitrogen fixation ability greatly (Jani et al. 2005). Water may also play important roles in the process of epiphytic nitrogen fixation in Ailao Mountain Forest.

Nitrogen fixation studies often extrapolate that acetylene reduction rates stem from one single sampling event to annual N fixation rates which helps facilitate comparison across sites and with other components of the N cycle (Reed et al. 2008).

We extrapolated the annual N fixation rates of the epiphyte community in Ailao Mountain Forest according to the extreme value recorded in our results, except the results in February. For there has been a drought during January and February 2006, the average rate increased about 100 times in November 2005 and March 2006.

If we used the average C_2H_4 production rate of samples in the sub-canopy layer in November 2005 to calculate the minimum and used the average rate of samples in the sub-canopy layer in October 2006 to calculate the max value, the annual N fixation rates would range between 0.027 and 2.24 kg $ha^{-1}year^{-1}$, which was higher than the result of 0.1 kg $Nha^{-1}year^{-1}$ in Costa Rica (Carpenter 1992) and close to the result of about 1.5–8 kg $Nha^{-1}year^{-1}$ in Colombia (Forman 1975). This result inspired us again to compare the amount of annual nitrogen which was 14.18 kg $Nha^{-1}year^{-1}$ imported by rainfall, 6.09 kg $Nha^{-1}year^{-1}$ by penetrative rain, and 0.02 kg $Nha^{-1}year^{-1}$ by stem flow (Qiu et al. 1998).

Hofstede (1993) reported that the epiphytic plant built a great nutrient storage as their abundant biomass. Compared with the former results (Qiu et al. 1998), the average nitrogen content of epiphytic plant was higher than the organs of seven kinds of dominant trees such as leaves, branches, stems, and roots and was also higher than the organs of dominant species in the shrub layer and the herb layer. The nitrogen storage of epiphytic plants in this forest was calculated to be about 194.38 kg ha^{-1}, which was about 14.00% of the nitrogen storage in arboreal layer plants and about 4.96 times higher than in the shrub layer and 11.87 times higher than in the herb layer (Qiu et al. 1998).

The living environment such as height and humidity could affect the nitrogen fixation ability of epiphytic plants. The organism substance circulation of forest ecosystems at different heights may also affect the nitrogen fixation activity of epiphytic community. Our samples were all collected under the height of 20 m, and epiphytic plants including lichen at a higher height may have higher level of nitrogen fixation ability, and maybe, the free living micro-organisms in the humus which were removed from our epiphytic samples also could fix nitrogen and would contribute greatly to the nitrogen amount fixed by epiphytic plants. These potentials would augment the nitrogen contribution by the epiphytic community. Our results should not be considered definitive annual rate; however, it reminds us of the role of the epiphytic plants in nitrogen cycle, which is still unclear in Ailao Mountain Forest.

The wide existence of nitrogen fixation ability among the epiphytic plants in Ailao Mountains gave us a new concept to study the nitrogen cycle in subtropical forests.

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Conflict of interest The authors declare that they have no conflict of interest.

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