



Response of non-vascular epiphytes to simulated climate change in a montane moist evergreen broad-leaved forest in southwest China

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ABSTRACT

Interest in the potential effects of global climate change on forest ecosystems is increasing, but little is known about their effects on canopy communities, even though their reliance on atmospheric moisture and nutrients suggest that they are sensitive to current predictions of climatic change. We conducted a field experiment to assess the potential impacts of predicted climate change on the growth and health of four common non-vascular epiphytes at three elevations in a subtropical montane moist evergreen broad-leaved forest in southwest China. Even slight changes in climate resulted in remarkably reduced rates of growth and detrimental effects on the health of the transplanted epiphyte species over 2 years. Non-vascular epiphytes in this forest type respond much more rapidly to changes in water availability than terrestrial trees. The non-vascular lichen, *Nephromopsis pallescens*, is highly sensitive to changes in moisture and temperature, and could be adopted as a climate change indicator. Non-vascular epiphyte species may be negatively affected or even severely damaged in the future in subtropical montane forests, as climate conditions are predicted to be warmer and drier. This experiment confirms previous model projections and implies that conservation efforts to maintain the stability and resiliency of montane forest ecosystem to climate change should include epiphyte communities.

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1. Introduction

Evergreen broad-leaved forests contribute to global biodiversity, and are important to the sustainable development of subtropical regions of China (Wang et al., 2005; Wu, 1980). Montane moist evergreen broad-leaved forests (MMEBFs) are a subgroup of evergreen broad-leaved forests, and occurs mainly in tropical and subtropical mountains at high altitude in Yunnan Province, south-western China (Wu, 1987). Due to the high rainfall, high relative humidity (RH), the presence of large trees, and absence of widespread human disturbance, the MMEBF located in the Ailao Mountains is especially rich in epiphytes, with 460 epiphytic species and an estimated biomass of 10.7 t ha⁻¹ (Li et al., 2011; Ma, 2009; Xu and Liu, 2005).

The world is warming, with increases in global average air temperature and widespread melting of snow and ice (IPCC, 2007). Further warming may occur if emissions of greenhouse gases con-

tinue at or above current rates (IPCC, 2007). Global climate models predict a declining trend of relative humidity (RH) over most tropical land surfaces (Foster, 2001). Even a slight rise in the concentration of CO₂ will increase the elevation at which clouds form in tropical montane forests (Still et al., 1999). In parallel with these global trends, over the past 40 years, the annual temperature has increased at a rate of 0.3 °C decade⁻¹ in Yunnan Province (south-western China) (Fan et al., 2011), while the air RH has shown a decreasing trend in tropical regions of Yunnan (He et al., 2007). Further, the annual temperature is predicted to increase by 2.2 °C and the annual precipitation to decrease by 130 mm by the 2050s, compared with the current condition in the MMEBF (Hijmans et al., 2005; Ramirez and Jarvis, 2008).

Climate change has triggered plant responses in many parts of the world, including shifts in species distribution and changes in physiology (Thuiller et al., 2005), and is gaining increasing attention worldwide (Jump and Penuelas, 2005; Ryan, 1991; Thuiller et al., 2005). Studies on impacts of climate change on epiphytes are scarce, even though they have been predicted as being sensitive to atmospheric changes because they are anchored in the forest canopy and lack access to water and nutrients on the forest floor or from the host vascular system (Benzing, 1998; Hietz, 1998; Gradstein, 2008; Nadkarni and Solano, 2002).

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Because non-vascular epiphytes are poikilohydric and lack roots and an outer waxy cuticle, they are probably more sensitive to changes in ambient climatic conditions than are vascular epiphytes. Model simulations by Ellis et al. (2007a) suggested that an epiphytic lichen (*Lecanora populicola* (DC) Duby) in the United Kingdom may expand in its potential range to future climate change. In the British Isles, lichen species in southern regions will increase in extent, while those in the north will decrease in response to future climate change (Ellis et al., 2007b). Some non-vascular epiphytes have already been affected by climate change in central Europe, where certain Atlantic and Mediterranean species have extended their ranges into north and north-eastern Europe in the last decades because of global warming (Frahm and Klaus, 2001). Translocation experiments in Bolivia indicated that global warming may influence the structure of epiphytic communities (Jácome et al., 2011).

Among the few studies that assessed the potential impact of climate change on non-vascular epiphytes, most evidence has been derived from modeling work (e.g. Ellis et al., 2007a, 2007b; Ellis et al., 2009). Empirical studies are needed to confirm model projections. Previous empirical studies have focused on either range shifts or community dynamics, with few addressing the specific influences related to climate change on the growth and health of non-vascular epiphytes. In this study, we transplanted three common cryptogamic epiphyte species (two bryophytes, one lichen) from high elevation to medium and low elevation sites and monitored their growth and health at regular intervals in a subtropical MMEBF in the Ailao Mountains. Another bryophyte species was monitored *in situ* at the three translocation sites. During the study period, southwest China experienced the worst regional drought event in the past 100 years from the end of 2009 to early 2010 (Qiu, 2010; Stone, 2010; Wang, 2010).

The three objectives of this study are to: (1) assess the potential impact of predicted climate change on the growth and health of four common non-vascular epiphytes in the MMEBF; (2) verify whether target species are affected by drought; and (3) assess the potential of the target species as indicators of climate change.

2. Material and methods

2.1. Study sites

We conducted this study in the Xujiaba region of south-western China (24°32'N, 101°01'E) in a protected section of a 5100 ha pristine MMEBF in Ailao Mountains National Nature Reserve (23°35'–24°44'N, 100°54'–101°01'E), at 2000–2600 m altitude (Li, 1983). The study site is affected by both the south sub-current of the west current from India and Pakistan and the southwestern monsoon, so it experiences a striking alternation of dry and wet conditions (Qiu and Xie, 1998). January and July are typically the dry and rainy season, respectively, while both April and October are typically the transition periods (Qiu and Xie, 1998). The following averages were recorded from the weather station in Xujiaba region between 2000 and 2010: average annual temperature, 11.1 °C (mean = 5.6 °C in January; 15.3 °C in July); mean annual precipitation, 1874 mm, with 87% of the rain in the rainy season (May to October); mean annual RH, 84%.

The forest is co-dominated by *Lithocarpus hancei* (Benth.) Rehder, *Castanopsis rufescens* (Hook.f. et Th.) Huang et Y.T. Chang, and *Lithocarpus xylocarpus* (Kurz) Markgr. (You, 1983). Canopy epiphytes are abundant, including 176 species of epiphytic bryophytes belonging to 38 families and 83 genera (Ma, 2009). The dominant species are *Homaliodendron flabellatum* (Sm.) Fleisch., *Plagiochila arbuscula* (Brid. ex Lehm. et Lindenb.) Lindenb., *Homaliodendron scalpellifolium* (Mitt.) Fleisch. (Ma, 2009). In addition,

51 epiphytic macrolichens have been recorded from 11 families and 21 genera (Li et al., 2011).

2.2. Experimental design and measurement

In October 2008, we established an elevational gradient (<300 m in altitude and 3 km in distance) to simulate climate changes (temperature and water availability). We established three sites (“high site”, 2550 m; “medium site”, 2400 m; “low site”, 2300 m). Rainfall, slopes, aspects, tree species composition, and forest structure were similar (Qiu and Xie, 1998). However, epiphytes at the high site were more abundant compared with the lower sites (Ma et al., unpubl. data).

To document water availability and air temperature, we measured the air temperature, air RH, and leaf wetness by placing an automatic weather station (Hobo U30, Onset Computer Corporation) at ca. 1.5 m height beneath the canopy at each study site. Microclimate measurements were carried out for 10 d each month (recorded every 30 min) in January, April, July, and October from 2010–2011.

We monitored epiphytes both *in situ* and that been transplanted from upper site to slightly warmer and dryer lower sites. We chose the net bag method for epiphytic bryophyte transplantation (Rosso et al., 2001). One common liverwort (*Bazzania ovistipula* (Steph.) Mizut.), and one common moss (*Trismegistia undulate* Broth. et Yas) were used for the translocation experiment as they were easily obtainable and present throughout the gradient (Ma, 2009). Bryophyte mats that were composed solely of the two target species were collected from tree trunks at the high site. After collection, mats were air dried to constant weight in the lab, and cleaned of litterfall, loose organic matter, and non-target species. We divided the mats into pieces (5.0 ± 0.5 g) and placed them into plastic net bags, closed, and tied to hosts with monofilament fishing lines (Fig. 1b). Thirty samples were prepared; 20 samples for transplantation to trunks of the same host species at the medium site and low site (10 per species per site), and 10 transplanted to the high site as control. We also dried five samples in a 60 °C oven for 24 h and re-weighed them to determine air-dry weight and biomass ratios. Each year, all transplants were taken to the lab, cleaned (mainly removing litterfall), and reweighed.

The health of all shoots were also ranked according to their appearance (Rosso et al., 2001): 0 = fully brown, dead looking; 1 = yellowish or with many brown patches (>50% brown); 2 = some brown or die back (10–50% brown); 3 = healthy and green (<10% brown).

H. flabellatum, an epiphytic bryophyte that grows extensively in the study region (Ma, 2009), was selected to monitor growth differentiation at different elevations. For each study site, 20 healthy shoots of *H. flabellatum* growing on trunks of *L. hancei* were tagged at about 10 mm from the apex of the shoot with a single thread of embroidery cotton at the start of the experiment (Mitchell et al., 2004). Then, the shoots were measured every 6 months using calipers (Fig. 1a).

One epiphytic foliose lichen (*Nephromopsis pallescens* (Schaer.) Y.S. Park) was selected as the target lichen species for translocation, as it was abundant and easy to sample. We used pendant transplants of thalli fragments of this lichen to assess the biomass increment in different climate conditions at different elevations following McCune et al. (1996). In early November 2008, lichen thalli were collected from the high site, and the outer lobes were used as transplants. The lichen fragments were air dried for 24 h at room temperature and weighed. Pieces (0.1–0.2 g) were attached to two to three cm nylon monofilament loop using a silicone sealant (Fig. 1c). After a further 24 h of air-drying, all thalli were re-weighed, including the weight of the device. For each species, 90 samples were transplanted to lower canopies in the three sites (30 samples

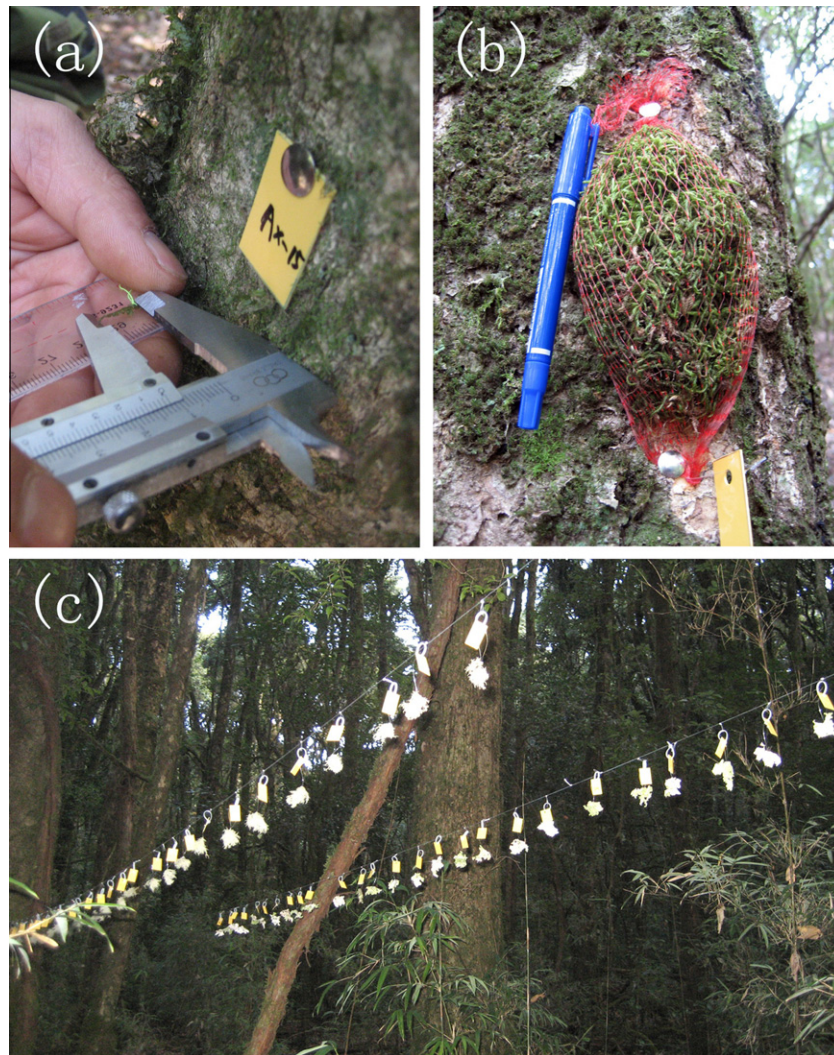


Fig. 1. Study methods and materials. (a) Shoot elongation measurement of *Homaliodendron flabellatum* in the field. (b) Photograph of net bag transplantation method of epiphytic bryophytes. (c) Photograph of pendent transplantation method of epiphytic lichens.

per site) in November 2008, after which samples were removed, transported to the lab and air-dried for 24 h before re-weighing, and then taken back to the field every 6 months for 2 years. Because the weight of air-dried lichens is affected by humidity and temperature, water content of thalli was adjusted using the reference sample method (Caldiz, 2004; McCune et al., 1996).

We ranked the health of each lichen thallus: 0 = fully brown, dead looking; 1 = with many brown patches (>50% brown); 2 = some brown or dieback (10–50% brown); 3 = healthy (<10% brown).

Relative measures of growth of the five species were calculated as:

$$RG = \frac{G_{ij}}{G_{hj}} \times \frac{G_{h0}}{G_{i0}} \quad (1)$$

G_{ij} : site average biomass or length (high, medium, or low) for a specific species at a specific time; G_{hj} : the average biomass or length for the species at the same time from the high site (as control). G_{h0} and G_{i0} : initial average biomass or length for the specific species been transplanted to the high site (as control) and site (high, medium or low), respectively.

2.3. Statistical analysis

Differences in growth and microclimate condition among different sites and observation periods were analyzed using repeated

measures GLM (Garson, 2008). Differences in growth among different sites within each observation period were analyzed with one-way ANOVA and multiple comparisons were conducted using Dunnett's or Game–Howell's post hoc tests. The categorical health data were analyzed with non-parametric methods (Kruskal–Wallis H). All analyses were conducted using the SPSS 16.0 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Microclimate

Repeated measure GLM showed significant effects of site over 1 year on temperature, RH, and leaf wetness (Table 1). Mean air temperature at the high site was 8.8 °C, which was significantly lower than temperature at the medium (9.7 °C) and low (10.6 °C) site. The air RH showed a reverse trend compared with air temperature, with mean values of 94.7%, 90.7%, and 88.7%, at the high, medium, and low sites, respectively. Mean leaf wetness at the high site (34.3) was significantly higher than the other two lower sites.

Repeated measure GLM showed significant effects of time (January, April, July, and October) on temperature, RH, and leaf wetness (Table 1). The dynamics of air temperature, RH, and leaf wetness followed similar seasonal patterns among the three elevations.

Table 1
Results of repeated measure GLMs for microclimate data among the three transplantation sites from April-2010 to January-2011.

Source	F	P
(A) Temperature		
Site	8.651	0.001
Time	118.554	<0.001
Site × time	0.087	0.954
(B) RH		
Site	6.142	0.006
Time	20.710	<0.001
Site × time	0.665	0.619
(C) Leaf wetness		
Site	4.870	0.016
Time	31.175	<0.001
Site × time	2.466	0.067

The highest mean air temperature, RH, and leaf wetness occurred in July 2010; the lowest temperature in January 2011, and the lowest RH and leaf wetness were both in April 2010 (Fig. 2).

Mean monthly temperatures during the drought of September, 2009–April 2010 were higher than the previous 9 years' mean values, whereas mean RH and total rainfall were lower than the corresponding mean values of 9 years (Fig. 3).

3.2. Response of growth and health of epiphytic bryophytes after transplants

We detected no significant differences at different elevations among the initial biomass of *Trismegistia undulata* ($F_{2,23} = 0.045$, $P = 0.956$) or *B. ovistipula* ($F_{2,17} = 1.844$, $P = 0.188$). Repeated measure GLMs showed that effect of time on the growth of *T. undulata*

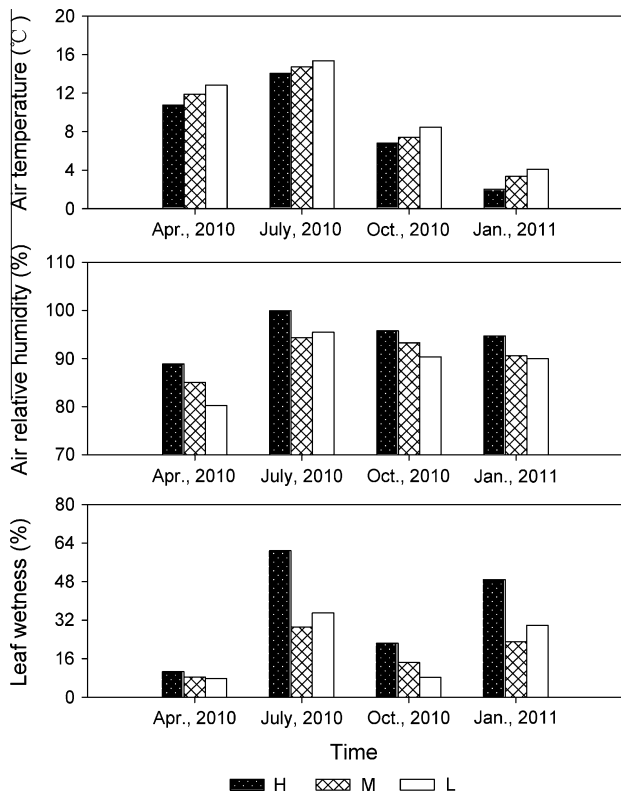


Fig. 2. Comparison of average air temperature, relative humidity, and leaf moisture among different sites in January, April, July, and October from 2010–2011. Notes: H, high site; M, medium site; L, low site.

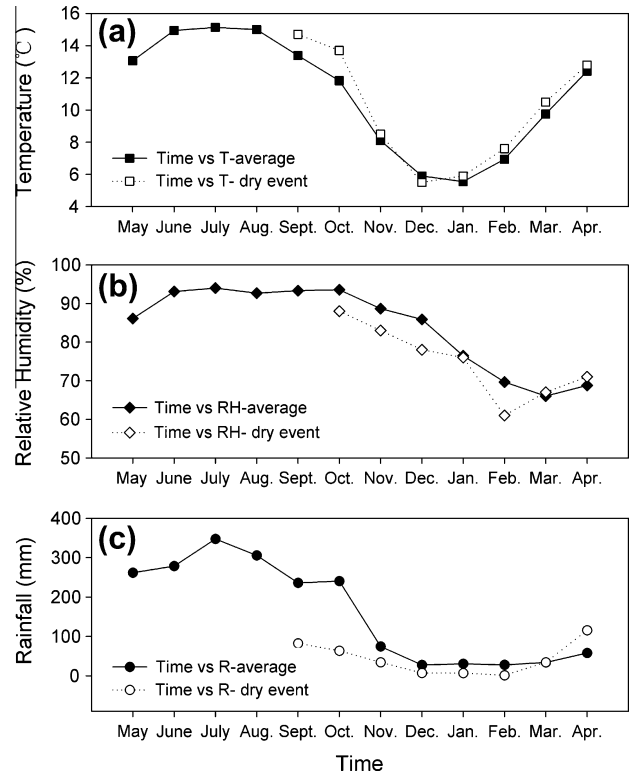


Fig. 3. Comparison of average air temperature, air relative humidity, and total quantum of rainfall between the period of the drought event (from September, 2009 to April, 2010) and 9 years' average values before the drought event (from 2000 to 2008) in Ailao Mountains. T_{ave} (RH_{ave} , R_{ave}) refers to average monthly temperature (relative humidity, rainfall) from 2000–2008; T_{dry} (RH_{dry} , R_{dry}) refers to monthly temperature (relative humidity, rainfall) during the dry event from September, 2009 to April, 2010.

ta was significant, while effects of site ($P = 0.067$) and interaction between site and time ($P = 0.073$) were not, but close to significant (Table 2). Significant effects of time and interaction between site and time were detected on growth of *B. ovistipula* (Table 2).

T. undulata grew fastest at the high site, and slowest at the low site (Fig. 4a and b). The mean biomass of *T. undulata* at the low site was significantly lower than at the high site the first year after transplantation (Fig. 4a and Table 3). Samples at all sites showed

Table 2
Results of repeated measure GLM for growth of different epiphytes (represented by shoot length for *Homaliodendron flabellatum* and biomass for the other three species) among the three transplantation sites from 2008 to 2010.

Source	F	P
(A) <i>Trismegistia undulata</i> Broth. et Yas		
Site	3.042	0.067
Time	4.419	0.018
Site × time	2.300	0.073
(B) <i>Bazzania ovistipula</i> (Steph.) Mizut.		
Site	1.935	0.175
Time	7.535	0.002
Site × time	4.112	0.008
(C) <i>Homaliodendron flabellatum</i> (Sm.) Fleisch.		
Site	1.924	0.158
Time	132.356	<0.001
Site × time	2.329	0.090
(D) <i>Nephromopsis pallescens</i> (Schaer.) Y.S. Park		
Site	7.336	0.002
Time	45.902	<0.001
Site × time	10.870	<0.001

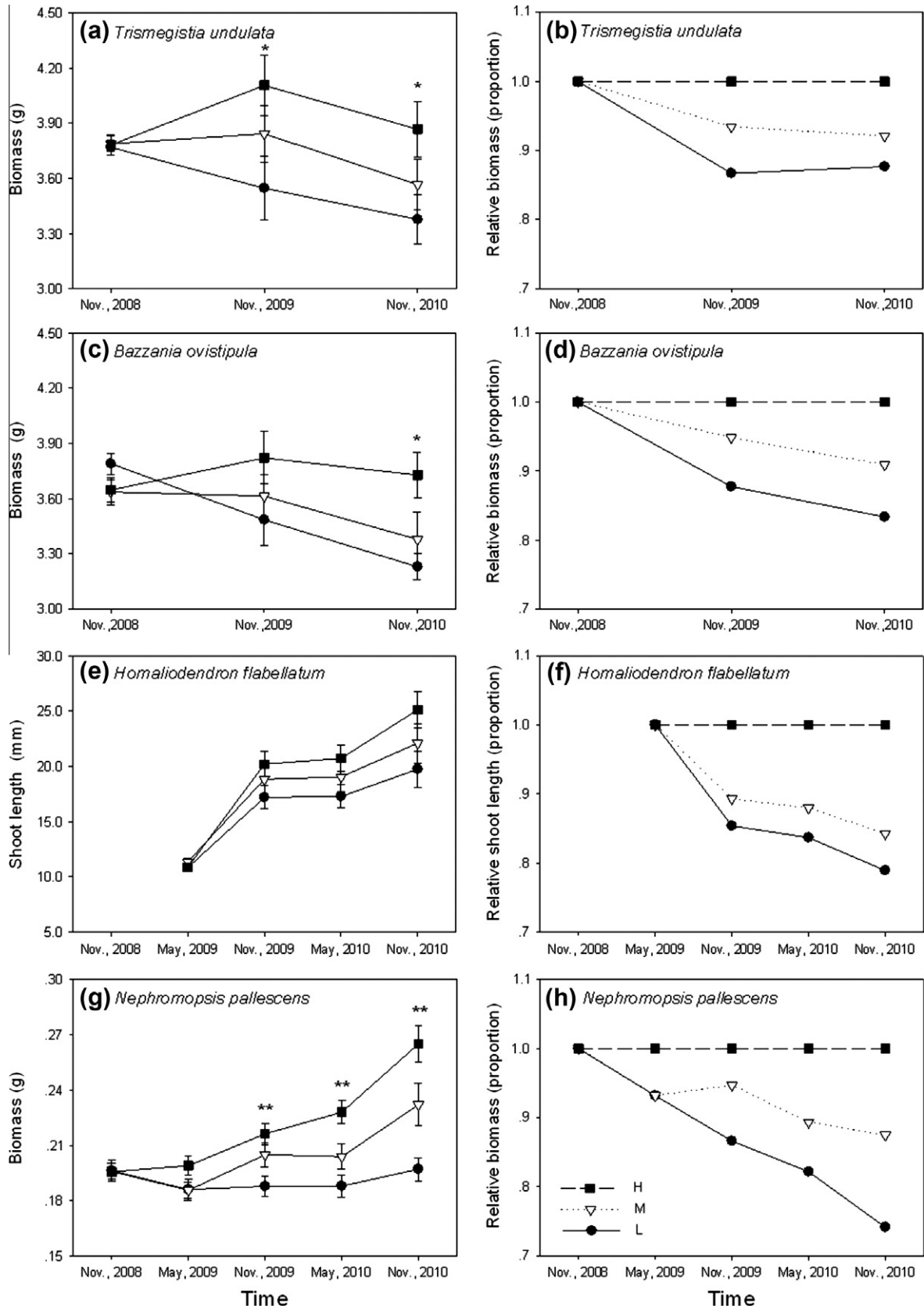


Fig. 4. Treatment effects of simulated climate change on growth of different epiphytes (represented by shoot length for *Homaliodendron flabellatum* and biomass for the other three species). Bars indicate \pm SE. Notes: H, high site; M, medium site; L, low site. * and ** represent differences among transplantation sites within the observation period are significant at the 0.05 level and the 0.01 level, using one-way ANOVA, respectively.

Table 3
Results of multiple comparisons (Dunnett's post hoc tests) of growth for different epiphytes (represented by shoot length (mm) for *Homaliodendron flabellatum* and biomass (g) for the other three species) among the three transplantation sites from 2008 to 2010. Note: Some of samples were lost or destroyed by animals during the 2 years' experiment, so the sample sizes (*n*) were different and all were less than the original sizes. H, high site; M, medium site; L, low site. Values are expressed as mean \pm SE.

Species	Site	<i>n</i>	Time				
			November, 2008	May, 2009	November, 2009	May, 2010	November, 2010
<i>Trismegistia undulata</i>	H	8	3.78 \pm 0.06	–	4.11 \pm 0.17	–	3.87 \pm 0.15
	M	9	3.79 \pm 0.04	–	3.84 \pm 0.16	–	3.57 \pm 0.14
	L	9	3.77 \pm 0.04	–	3.55 \pm 0.17*	–	3.38 \pm 0.14*
<i>Bazzania ovistipula</i>	H	6	3.65 \pm 0.07	–	3.82 \pm 0.14	–	3.73 \pm 0.12
	M	7	3.64 \pm 0.07	–	3.61 \pm 0.12	–	3.38 \pm 0.15
	L	7	3.79 \pm 0.06	–	3.49 \pm 0.14	–	3.23 \pm 0.07*
<i>Homaliodendron flabellatum</i>	H	16	–	10.9 \pm 0.4	20.2 \pm 1.1	20.7 \pm 1.2	25.1 \pm 1.7
	M	18	–	11.4 \pm 0.3	18.8 \pm 1.3	19.0 \pm 1.3	22.1 \pm 1.8
	L	15	–	10.8 \pm 0.4	17.2 \pm 1.1	17.3 \pm 1.1	19.8 \pm 1.6
<i>Nephromopsis pallescens</i>	H	19	0.196 \pm 0.005	0.199 \pm 0.005	0.216 \pm 0.006	0.228 \pm 0.006	0.265 \pm 0.010
	M	18	0.196 \pm 0.005	0.186 \pm 0.004	0.205 \pm 0.007	0.204 \pm 0.007*	0.232 \pm 0.012*
	L	17	0.196 \pm 0.006	0.186 \pm 0.006	0.188 \pm 0.005**	0.188 \pm 0.006**	0.197 \pm 0.006**

* Significant at the 0.05 level.

** Significant at the 0.01 level.

negative growth rate during November, 2009–2010 (Fig. 4a). The initial samples were all in very good health for *T. undulata*; however, health of samples in medium and low sites markedly deteriorated, with parts of transplants turning brown or dying back the first year after transplantation (Fig. 5a). Health of *T. undulata* showed significant differences among sites after 2 years (Kruskal–Wallis $H \chi^2 = 11.607$, $P < 0.01$). Samples in the low site severely deteriorated (Fig. 5a).

B. ovistipula responded to simulated climate change in a similar way as *T. undulata*, but the difference in mean biomass of *B. ovistipula* between the low site and the high site was significant during the second year after transplantation (Fig. 4c and d). However, in

spite of the obviousness of the differences, health of *B. ovistipula* did not differ significantly (Fig. 5b).

3.3. Response of growth of epiphytic bryophytes in situ

We detected no significant differences in initial and final shoot lengths of *H. flabellatum* at different elevations ($F_{2,46} = 0.715$, $P = 0.495$). Repeated measure GLM showed a significant effect of time on growth of *H. flabellatum*, but effect of site was not significant (Table 2), although measurable differences were detected (Fig. 4e and f and Table 3). Mean length of samples at different elevations showed almost no growth from November 2009 to May 2010, even for samples at the high site (Fig. 4e).

3.4. Response of growth and health of epiphytic lichens after transplants

We detected no significant differences at different elevations among the initial biomass of the samples of *N. pallescens* ($F_{2,51} = 0.004$, $P = 0.996$). Repeated measure GLMs showed significant effects of site and time, and also significant interaction between site and time on growth of *N. pallescens* (Table 2).

Samples of *N. pallescens* grew best at the high site, followed by samples at the medium site. Transplants at the low site showed almost no growth and poor health after transplantation (Figs. 4g and 5g). Six months after transplantation, there was no significant difference in growth among the three sites ($F_{2,51} = 2.241$, $P = 0.117$). Six months after this, we detected significant differences among different elevations ($F_{2,51} = 5.709$, $P = 0.006$). Biomass of *N. pallescens* markedly increased at the high and medium sites, but only slightly at the low site from May to November, 2009. Further, differences of biomass grew greater among different elevations in the following year (Fig. 4g and h and Table 3). Significant differences in health rank of *N. pallescens* occurred during dry seasons (May 2009, Kruskal–Wallis $H \chi^2 = 18.579$, $P < 0.01$; May, 2010, Kruskal–Wallis $H \chi^2 = 13.723$, $P < 0.01$) (Fig. 5c).

4. Discussion

4.1. Response of non-vascular epiphytes to simulated climate change

Results of the microclimate measurement confirmed that air temperature decreased, but water availability increased with altitude rising. The mean temperature increase by 1.8 °C and RH de-

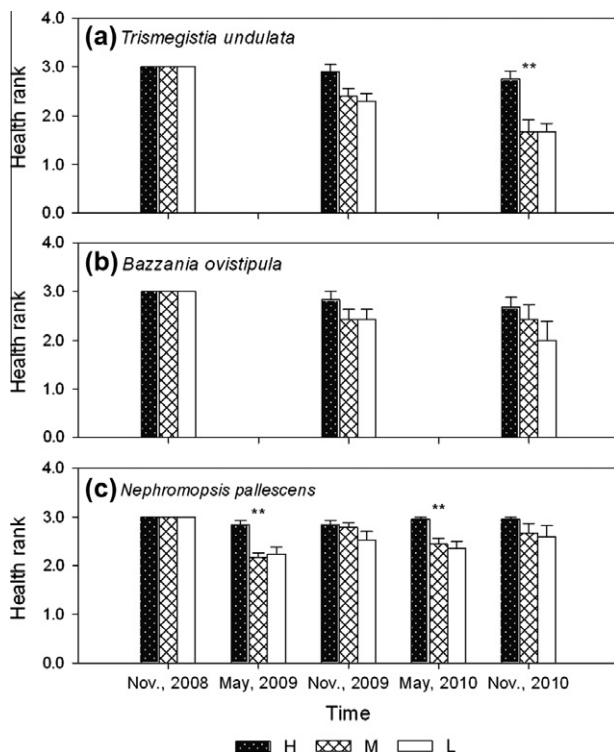


Fig. 5. Treatment effects of simulated climate change on health rank of different epiphytic species. Note: H, high site; M, medium site; L, low site. Bars indicate \pm SE. ** Indicates that differences among transplantation sites within the observation period are significant at the 0.01 level using Kruskal–Wallis H 's non-parametric test.

crease by 6% in the low site compared with that in the high site during the study period. As was mentioned above, the MMEBF studied here is predicted to become warmer and drier (Hijmans et al., 2005; Ramirez and Jarvis, 2008), the experimental exposure of epiphytes from high site to lower sites can be considered a likely proxy for estimating the effects of future global climate change in the study region.

The simulated climate change significantly negatively affected the growth and health of most non-vascular epiphytes studied here within 2 years (Table 3 and Figs. 4 and 5). Similarly, epiphyte mats collected from an upper site were transplanted to lower sites (from 1480 to 1410 and 1330 m) in Costa Rica, which were naturally exposed to smaller amounts of cloud water (Nadkarni and Solano, 2002). One year later, deterioration of the entire epiphyte mat was apparent (Personal communication). In Bolivia, branches covered with dense bryophyte mats were transplanted to lower altitudes (from 3000 m to 2700 m and 2500 m). The relative abundance of species in the community had been altered significantly 2 years later (Jácome et al., 2011). The translocation experiments using a space-for-time gradient confirmed the sensitivity of non-vascular epiphytes to climate change.

This result could be explained in two ways. First, higher temperatures consistently lead to higher respiration rates (Sillett and Antoine, 2004). Second, epiphytic bryophytes and lichens are poikilohydric, losing water and thus photosynthesis capacity quickly when the RH is low, with photosynthesis capacity resuming only if they are rehydrated (Sillett and Antoine, 2004). This situation is exacerbated by hydration dynamics (dry days and wet nights). As a result, many non-vascular epiphytes are incapable of the high photosynthetic rates needed to overcome respiratory energy losses under warmer, drier circumstance.

Other studies have also documented the sensitivity of non-vascular epiphytes to climate change, and that even slight shifts in climate conditions may have negative consequences. In Europe, Frahm and Klaus (2001) ascribed the range extension of Atlantic and Mediterranean bryophyte species into the north and north-east in the last decades to global warming; simulations predicted that many epiphytic lichens will shift their original ranges in response to future climate change (Ellis et al., 2007a, 2007b, 2009). In the Netherlands, the majority of subtropical lichens adapted to warm environments appeared to be increasing, but some arctic-alpine/boreo-montane species adapted to cold environments decreased due to global warming in the 1990s (Aptroot and Van Herk, 2007; Van Herk et al., 2002).

4.2. Response of epiphytes to drought events

Global atmospheric and water circulation have been altered, which further induces changes in rainfall patterns at global and regional scales (Trenberth, 1999). Predictions include: increase drought frequency, prolong drought period, and aggravate drought intensity according to climate models such as CCM0 (Easterling et al., 2000; Wetherald and Manabe, 1999). Increased drought is likely to become the most detrimental aspect of climate change for epiphytes that live in cool and wet forests (Zotz and Bader, 2009).

Gradstein (2008) proposed that drought had directly deleterious effects on non-vascular epiphytes in cloud forests, which was also true for epiphytic bryophytes in our subtropical moist forest. Our measurements showed that all *H. flabellatum* from three different elevations grew very little during the dry season of 2009–2010 (Table 3). However, we cannot distinguish whether the decline of growth was caused by the drought during this period (Fig. 3), or if it was a seasonal feature because we measured only one growth period. Nevertheless, *T. undulata* and *B. ovistipula* exhibited negative growth rates, with a quantitative decline in health between

November 2009 and November 2010, in contrast to positive growth rates between November 2008 and November 2009 (Table 3). We suggest that this could be attributed to severe dryness during this period (Fig. 3). Non-vascular epiphytes lose water quickly in dry air, which negatively affects their photosynthetic capacity. Under severe drought, photosynthesis of epiphytes cannot resume because they cannot obtain sufficient atmospheric water. This may lead to an imbalance in their annual carbon production, and thus the negative growth rate we observed. However, *N. pallescens* samples that we transplanted to the high (wettest) site showed a positive growth during the period of severe dryness (Table 3). This indicates that the chlorolichen *N. pallescens*, may be more tolerant of desiccation than bryophytes (see Sillett and Antoine, 2004). Nevertheless, water availability has been suggested to be the overriding environmental factor determines the composition and distribution of poikilohydric epiphytes (Bates et al., 2004; Sillett and Antoine, 2004).

This study corroborates the pattern of epiphytes being more abundant in a tropical lowland cloud forest compared with a nearby lowland rain forest in French Guiana, which was attributed to the prolonged availability of higher RH and the additional input of liquid water through fog in the cloud forest (Gehrig-Downie et al., 2011; Normann et al., 2010). Even in forest ecosystems less dependent on continuous moisture input, species composition of epiphyte communities changed drastically when the environment became drier following disturbance (Gradstein, 1992). Although non-vascular epiphytes may obtain water through interception of cloud water droplets from moving air in periods of low rainfall, and respond to short term drought by reducing physiological activity (León-Vargas et al., 2006; Sillett and Antoine, 2004), they may be severely damaged if drought lasts for a long period. Future research should investigate this “tipping point”.

Non-vascular epiphytes in the montane moist forest were under water shortage during the 2009–2010 drought. However, trees in the forest did not experience water deficits during that period (Qi et al., 2012). Trees can survive in dry seasons or droughts by absorbing stored underground water. In contrast, epiphytes have little or no buffered pools of moisture and nutrients, so they are more responsive to even subtle changes in climate than are terrestrially rooted plants (Nadkarni and Solano, 2002). We infer that non-vascular epiphytes will respond much sooner to changes in the water cycle, especially dryness, than their terrestrial counterparts in the subtropical montane moist forests of south-western China.

4.3. Bio-indicators

Epiphytes have been proposed to be potentially excellent indicators for even slight shifts in climatic patterns (Benzing, 1998; Lugo and Scatena, 1992). The chlorolichen *N. pallescens* showed the most significant and largest differences in growth and health after having been exposed to warmer, drier conditions. We thus propose that *N. pallescens* could be a potential climate change indicator in the subtropical MMEBF.

The mean biomass of epiphytic bryophytes, both *T. undulata* and *B. ovistipula*, at the low site was significantly lower than at the high site after transplantation for 2 years. In addition, growth of these two bryophytes was negatively affected by the severe drought from the end of 2009 to early 2010. These indicate that *T. undulata* and *B. ovistipula* are susceptible to climate change. However, there were no significant effects of site on growth of *H. flabellatum*, *T. undulata* and *B. ovistipula* (Table 2), implying that the three bryophytes are not robust enough to be good indicators of climate change. Considering the pendant life-form favors habitats with high atmospheric humidity (Bates, 1998), we suggest that pendent epiphytes might be used as indicators.

4.4. Implications

Our ability to measure, predict, and prepare for the growing effects of climate change on tropical ecosystems is hindered by our limited knowledge of climate change impacts (Laurance et al., 2011). This study is the first attempt to assess the possible impact of climate change on the growth and health of non-vascular epiphytes in a subtropical MMEBF. Non-vascular epiphytes in this forest are susceptible to simulated climate change and may be more vulnerable than terrestrial trees. This study at least confirms previous model projections and compensates for the shortage of empirical evidence on the sensitivity of epiphytic flora in response to climate change. As climate conditions in the MMEBF is predicted to become warmer and drier by the 2050s (Hijmans et al., 2005; Ramirez and Jarvis, 2008), many non-vascular epiphyte species may be negatively affected or even face extinction. However, epiphytes with strong dispersal ability may shift their distribution to cooler, moister habitats. The montane forest canopy communities in tropical and subtropical regions might represent one of the world's best biological assemblages for the direct monitoring of climate change and provide an early warning of biological outcomes related to climate change.

Adverse effects of climate change on epiphytes cannot be considered in isolation (Zotz and Bader, 2009). Because epiphytes play important roles in hydrological and nutrient cycles of the forest ecosystem, and facilitate other plant and animal life in forest canopies (Benzing, 1998; Zotz and Bader, 2009), deterioration of epiphytes induced by climate change may have cascading negative effects on the whole forest ecosystem. Thus, conservation efforts to maintain the stability and resiliency of tropical or subtropical montane forest ecosystem to climate change should include epiphyte communities.

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