Sains Malaysiana 43(8)(2014): 1119–1125

Effect of Elevation and Canopy Condition on Morphological Traits and Leaf Fluctuating Asymmetry of a Bamboo, *Chimonobambusa utilis* in Jinfo Mountain Nature Reserve, Southwest China

(Kesan Ketinggian dan Keadaan Kanopi ke atas Sifat Morfologi dan Asimetri Turun-Naik Daun Buluh, *Chimonobambusa utilis* di Gunung Simpan Semula Jadi Jinfo, Barat-daya China)

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ABSTRACT

Due to widespread distribution of dwarf bamboo, Chimonobambusa utilis*, in mountain environment, the effects of elevation (low and high) and canopy condition (forest understorey and forest edge) on the clonal morphology and leaf fluctuating asymmetry were investigated in an evergreen broadleaves forest of Jinfo Mountain Nature Reserve. Elevation and canopy condition were significant for all morphological traits of* C. utilis *(except for effect of elevation on node number under branch). Traits of clonal morphology such as height, basal diameter, height under branch tended to be higher in forest understorey and in high elevation. Forest understorey in high elevation was favour of shooting number. Interaction of elevation and canopy conditions had a significant effect on growth of node. Single leaf area (SLA) and all indices of fluctuating asymmetry were significantly higher in low elevation than that in high elevation of forest understorey. Thus, elevation and canopy condition formed environmental stress that lead to the adaptation of morphological traits and leaf fluctuating asymmetry of* C. utilis *populations to mountain forest habitats.*

Keywords: Chimonobambusa utilis*; evergreen broadleaves forest; fluctuating asymmetry; morphological traits; specific leaf area*

ABSTRAK

Disebabkan oleh taburan meluas buluh kerdil, Chimonobambusa utilis *dalam persekitaran gunung, kesan ketinggian (rendah dan tinggi) dan keadaan kanopi (hutan bawah kanopi dan tepi hutan) pada morfologi klon dan asimetri turun-naik daun telah dikaji dalam hutan malar hijau daun besar di Gunung Simpan Semula Jadi Jinfo. Ketinggian dan keadaan kanopi adalah penting bagi semua ciri morfologi* C. utilis *(kecuali kesan ketinggian pada bilangan buku di bawah dahan). Ciri morfologi klon seperti ketinggian, diameter bes, ketinggian di bawah dahan cenderung untuk menjadi lebih tinggi di dalam hutan bawah kanopi dan ketinggian tinggi. Hutan bawah kanopi dalam ketinggian tinggi adalah memihak kepada bilangan pucuk. Interaksi ketinggian dan kanopi keadaan mempunyai kesan yang besar ke atas pertumbuhan buku. Keluasan daun tunggal (SLA) dan semua indeks turun naik ketidakseimbangan adalah lebih tinggi pada ketinggian yang rendah berbanding di ketinggian tinggi bawah kanopi hutan. Oleh itu, ketinggian dan keadaan kanopi membentuk tekanan alam sekitar yang membawa kepada ubahsuaian ciri morfologi dan asimetri turun-naik daun* C. utilis *bagi populasi habitat hutan gunung.*

Kata kunci: Chimonobambusa utilis; *hutan malar hijau daun besar; keluasan daun khusus; sifat morfologi; turun naik asimetri*

INTRODUCTION

Bamboos, with extreme density and wide range of distribution, often grew in habitats from open environments to forest understories and extended from broadleaved forest in the low elevations till conifer forest on high mountains (Wang et al. 2009, 2006). Elevation and forest canopy characteristics might be the important determinants of bamboo distribution and dispersal in mountain environments. Forest canopy characteristics (composition and density) affected patterns of resource availability (i.e. light, water, soil nutrients) on the forest floor, which influence bamboo growth and morphology (Taylor et al. 2004; Wang et al. 2012). On the other hand, climatic conditions change with altitude (along with exposure and slope), resulting in a patchy distribution of microhabitats, which can lead to major modifications in selection pressure on plant life-history traits, such as traits of clonal morphology and leaf (Pluess & Stöcklin 2005). Clonal growth was recognized as noticeable adaptations to various climatic conditions and patchy nutrient in mountain environments (Wang et al. 2012; Weppler & Stöcklin 2005). Due to their clonal life history, bamboos may optimize the efficiency of light and water use in their growth either by morphological plasticity or by clonal integration (de Kroon & Hutchings 1995). Generally, traits of clonal morphology were highly plastic in response to different environments (Wang et al. 2013; Weppler & Stöcklin 2005).

Simultaneously, leaf traits, such as specific leaf area (SLA, a relative measure of leaf thickness and density) and fluctuating asymmetry (FA) can be used as rapid and diagnostic indicators to stressful conditions. Since the left and right sides of a bilaterally symmetrical trait develop under the control of the same genes, minor deviations from perfect symmetry actually represent developmental instability (Cornelissen et al. 2004). FA is defined as a slight, nondirectional, deviation from perfect symmetry of a bilateral character, due to genetic and/or environmental stress (Palmer & Strobeck 1986). Many studies have demonstrated that individual- and population-levels of bilateral FA can be used as a measure of the severity of stress, such as elevation (Albarrán-Lara et al. 2010; Hagen et al. 2008), forest conditions (Henríquez et al. 2009; Wilsey et al. 1998), disturbance of herbivory or defoliation (Cornelissen & Stiling 2005; Cornelissen et al. 2004) and environmental pollution (Wuytack et al. 2011). Leaf fluctuating asymmetry has been documented in many environmental studies to examine the effects of environmental stress on plant leaf. Also, specific leaf area (SLA), a relative measure of leaf thickness and density, can emerge a high variability by habitat conditions and stress. Shrubland, desert and woodland species have an extreme low SLA, since drought, high light condition and nutrient limitation all hampered their growth (Poorter et al. 2009). Thus, plants in mountain forest with change of elevation and canopy may lead low SLA due to the variation of light, humidity and nutrient.

In mountain environment, dwarf bamboo *Chimonobambusa utilis*, within an altitudinal belt between 1300 m and 2200 m, is widespread in the evergreen broadleaves forest and forest edge of Jinfo Mountain Nature Reserve, southwest China. Due to their wide habitats, we try to better understand the effects of elevation and canopy condition on clonal morphological and leaf fluctuating asymmetry of dwarf bamboo, *C. utilis*, in an evergreen broadleaves forest of Jinfo Mountain. Specifically, we try to answer the following questions: How do clonal morphological traits of *C. utilis* vary in response to the elevation (low and high) and canopy condition (understorey and forest edge)? and how do SLA and FA of *C. utilis* understorey change with elevation stress?.

Materials and Methods

STUDY SPECIES

Chimonobambusa utilis (Keng) Keng f. is a dwarf bamboo, distributes widely in mountain forest conditions of southwest China. Shoots of *C. utilis*, being a special product with a history of 900 years, is a key industry in regional economics in Chongqing. Its annual production is 15000 t (output value USD 24,000,000), which takes the 42.8% of national production of shoots in *Chimonobambusa* genus. Clonal growth by rhizomes is the only way to its spread ramets during unflowering period. Following colonization by vegetative ramets, the populations and shoots production of *C. utilis* develop a large number of understorey patches in evergreen and deciduous broadleaved forest, forest gap and forest edge.

STUDY SITE AND DESIGN OF THE SURVEY

The study area was located in Jinfo Mountain Nature Reserve in Chongqing city, Southwest China. It belongs to subtropical humid monsoon climate. *C. utilis* populations were mainly distributed in forest understorey and at the forest edge of evergreen broadleaved forest from 1450 m to 2050 m a.s.l. Sites in low elevation (1500 m) (29°00′44″N, 107°08′39″E) and high elevation (2000 m) (29°0′17″N, 107°11′34″E) (with a distance of 5 km) were chosen for its wide distribution. Measurement was mainly conducted in the following two canopy conditions, forest edge and forest understorey of evergreen broad-leaved forest, in both elevations (Table 1) in late August 2011 and 2012 when the vegetation was mostly developed and the annual growth and shooting of *C. utilis* reached the stable stage. Sites of forest edge were mainly the edge of evergreen broadleaved trees such as *Castanopsis platyacantha*, *Quercus engleriana*, *Cyclobalanopsis* sp. and *Lithocarpus glabra*. Sites of forest undersory consist of the same tree species and with a canopy cover of 75-80% (Table 1). The forest floor is mainly covered with *C. utilis*.

In this study, canopy density in each gap and leaf area index was measured by the LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, USA). Each canopy type was composed of four quadrats of 3×3 m, in which 12 living culms of *C. utilis* (with a distance of 5 m) were selected for measurements. Characteristics of morphology (height, basal diameter, height under branch, node number, branch number, node number under branch, node length and shooting number) and fluctuating asymmetry of leaves (single leaf area, specific leaf area, fluctuating asymmetry based on leaf area, fluctuating asymmetry based on leaf width and composite fluctuating asymmetry index) were measured. Images of leaves of each culm were obtained and total leaves we scanned using a Umax Scanner (Microtek, China).

FLUCTUATING ASYMMETRY

In sites of forest understorey of low and high elevation, 100 fully developed and undamaged leaves were selected to calculate fluctuating asymmetry (FA), single leaf area and specific leaf area (SLA). After harvest, each leaf was sliced along the middle of the mid vein and the surface area of both right (RA) and left (LA) and leaf width of both right (RW) and left (LW) (as the widest perpendicular distance from the leaf margin to the midrib lamina sides) were measured by Image-Pro Plus 6.0 software (accuracy 0.01 mm).

RA (cm^2) and LA (cm^2), RW (cm) and LW (cm) were used to assess leaf area fluctuating asymmetry (FAA) and leaf width fluctuating asymmetry (FAW), respectively. The

TABLE 1. General situation of sites

Sites	Altitude (m)	Slope (°)	Canopy cover (%)	Leaf area index	Density of *C. utilis* (no./m^2)	Dominant canopy species
Understorey	1500	7-15	79.20±2.48	3.09±0.18	4.04±0.35	*C. platyacantha, Q. engleriana* and *C. sp*
Forest edge			24.34±1.32	0.95±0.13	3.22±0.53	/
Understorey	2000	4-9	75.55±1.93	2.88±0.09	3.80±0.26	*C. platyacantha, C. sp*. and *L. glabra*
Forest edge			20.90±0.81	0.77±0.06	3.90±0.37	/

accuracy of the measurements was tested involving FA analyses (Kozlov et al. 2009). One hundered randomly collected leaves were re-measured three times within 1% measurements error for leaf width and leaf area. However, 69 and 94 leaves from low and high elevation, respectively, were employed in FA analysis due to testing of error analysis. To compare *Chimonobambusa* asymmetry understorey between low and high elevation, two indices of FA were used (Palmer & Strobeck 1986):

$$\text{Index }1=\frac{\sum\left|R_i-L_i\right|}{N} \tag{1}$$

$$\text{Index }2=\frac{\sum\left[\dfrac{\left|R_i-L_i\right|}{\left(R_i+L_i\right)/2}\right]}{N} \tag{2}$$

where R_i is the value of the right side, L_i is the value of the left side and N is the number of leaves in measurements. Index 1 is the most intuitive asymmetry measure (Cornelissen & Stiling 2005) and index 2 is size-scaled, correcting for the fact that asymmetry can be size-dependent (Cornelissen et al. 2004).

DATA ANALYSIS

The Kolmogorov-Smirnov test revealed that the (R-L) distribution of leaf area and leaf wide from normality to test fluctuating asymmetry (FA) (Wuytack et al. 2011). We employed two-way ANOVA and independent-samples *t* test for effect of elevation (low and high) and canopy condition (forest understorey and forest edge) on morphology and for effect of elevation on characteristics of fluctuating asymmetry of leaves of *C. utilis* understorey. If necessary, the data were square-root transformed prior to meet the assumptions of normality and homogeneity of variance. If there was a significant effect, a multiple comparison *Tukey* test was used to determine significant differences between treatments. Differences were considered significant at $p<0.05$ level. A box-plot was also employed to compare fluctuating asymmetry of leaves between two elevations. SPSS statistical package was used for all analyses (SPSS 11 Copyright: SPSS Inc.). Figures were drawn by Origin Pro 7.0 (software).

RESULTS

EFFECT OF ELEVATION AND CANOPY CONDITIONS ON MORPHOLOGICAL TRAITS OF *C. UTILIS*

Elevation was significant for all morphological traits of *C. utilis* except for node number under branch ($p<0.05$) (Table 2). Height, basal diameter, height under branch and node length tended to be higher in high elevation than in low elevation regardless of understorey or forest edge ($p<0.01$) (Table 2; Figure 1). The canopy conditions

TABLE 2. ANOVA summary of the effect of elevation, canopy condition and interaction on morphological traits of *C. utilis* in field experiment in Jinfo Nature Reserve

Morphology	d.f.	*F* ratio	*P*-value	*F* ratio	*P*-value	*F* ratio	*P*-value	*F* ratio	*P*-value
		Height		Basal diameter		Height under branch		Node number	
Elevation	1	51.738	<0.001***	135.414	<0.001***	17.927	<0.001***	12.389	0.001**
Canopy condition	1	78.195	<0.001***	49.787	<0.001***	51.367	<0.001***	70.845	<0.001***
Elevation ×Canopy	1	0.001	0.980	0.157	0.694	0.669	0.417	21.279	<0.001***
Whole Model	3	48.790	<0.001***	67.296	<0.001***	24.719	<0.001***	48.329	<0.001***
Morphology	d.f.	Branch number		Node number under branch		Node length		Shooting number	
Elevation	1	7.020	0.011*	0.141	0.709	44.366	<0.001***	4.253	0.045*
Canopy condition	1	9.358	0.004**	60.757	<0.001***	13.026	0.001**	8.248	0.006**
Elevation ×Canopy	1	16.463	<0.001***	0.009	0.926	17.301	<0.001***	2.044	0.160
Whole Model	3	15.920	<0.001***	21.819	<0.001***	21.132	<0.001***	6.605	0.001

*****$p<0.001$, **$p<0.01$, *$p<0.05$

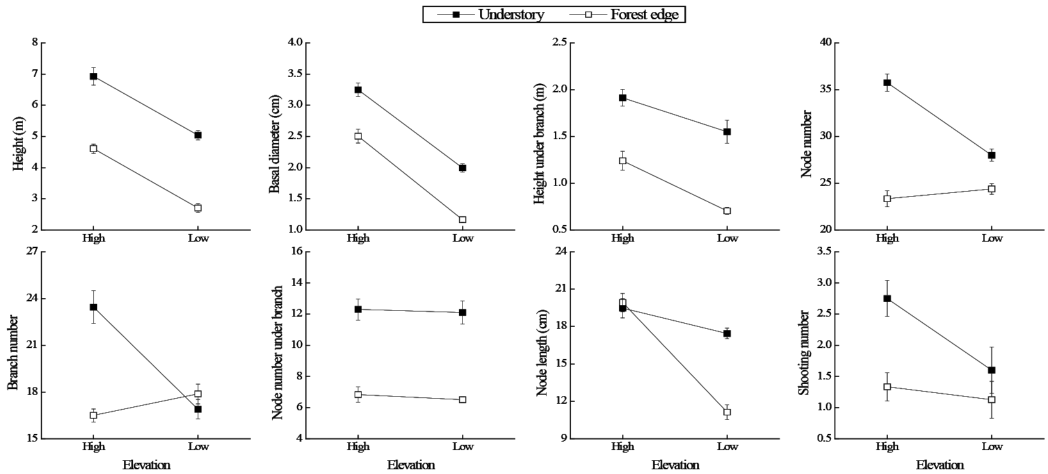

FIGURE 1. Mean number of morphological traits (± SE) of *C. utilis* populations in canopy conditions of forest understorey and forest edge in high (2000 m) or low elevation (1500 m)

had a significant effect on all morphological traits of *C. utilis* (p<0.01). Height, basal diameter, height under branch, node number and node number under branch were significantly higher in forest understorey than in forest edge regardless of low or high elevation (p<0.01) (Table 2; Figure 1). Interaction of elevation and canopy conditions had a significant effect on branch number, node number and node length (p<0.001). Node number, branch number and shooting number in high elevation were significantly higher than in low elevation in forest understorey (p<0.01). However, these parameters had no significant differences between two elevations in forest edge (Table 2; Figure 1). Branch number and shooting number in forest understorey were significant higher than that of forest edge in high elevation (p<0.01). However, these parameters had no significant differences between two canopy conditions in low elevation. Moreover, node length indicated an opposite trend comparing with the parameters of branch number and shooting number (Table 2; Figure 1).

LEAF FLUCTUATING ASYMMETRY OF *C. UTILIS* IN FOREST UNDERSTOREY OF DIFFERENT ELEVATION

The Kolmogorov-Smirnov test showed that the (R-L) distribution of absolute and size-scaled leaf width and leaf area significantly deviated from normality (p<0.05) and Shapiro-Wilk test also showed significant different (p<0.05), which indicated the asymmetry can be defined as FA (fluctuating asymmetry). Box plots of leaf fluctuating asymmetry and single leaf area of *C. utilis* in forest understorey indicated that the data distribution were in the upper for population of low elevation and in the lower for high elevation (Figure 2). Simultaneously, mean number of single leaf area, absolute fluctuating asymmetry (index 1 of FAW and FAA) and size-scaled fluctuating asymmetry (index 2 of FAW and FAA) were significantly higher, while specific leaf area was significantly lower in low elevation than in high elevation of forest understorey (Table 3).

DISCUSSION

The results confirmed elevation (low and high) and canopy condition (understorey and forest edge) had highly significant effects on almost all morphological traits of *C. utilis*. The parameters that culm height, basal diameter, height under branch and node length at high elevation (2000 m) was higher than those at low elevation (1500 m), which implied that elevation of 2000 m might be optimal where the moisture and temperature conditions are most favorable for bamboo regeneration (Li et al. 2013). *C. utilis* population mainly distributed in elevation of 1500-2000 m though it had a wide range of distribution in evergreen broadleaved forest from the low elevation (1000) till on high mountains (2100 m). Climatic conditions (temperature and moisture) changed, to some extent, rainfall and slope location varied with altitude, resulting in different micro-climate habitats (Pluess & Stöcklin 2005; Wang et al. 2009). At elevation of 2000 m in Jinfo Mountain, 20% more rainfall and moisture emerged in growth season, which could be ideal for bamboo growth and morphological development. Slope (7-15°) and low slope location in elevation of 1500 m might hinder the resource utilization and its clonal growth. Previous study on dwarf bamboo indicated that the aspect, angle of the slope and valley bottoms could affect the amount of light that reaches the canopy (Suzaki et al. 2005). Study on arrow bamboo indicated that elevation and canopy cover had highly significant effects on seedling density of bamboo. Bamboo growth was highest and showed the best regeneration at middle elevations (2800-3000 m) and under medium to medium-high canopy cover (0.41-0.60 and 0.61-0.80) (Li et al. 2013). Bamboo height and diameter were not significant difference in elevation 3200-3500 m for *Bashania spanostachya* whereas it decreased in higher elevation 3600-4000 m due to the change of moisture and temperate conditions (Wei et al. 1999). Thus, integrative habitats of

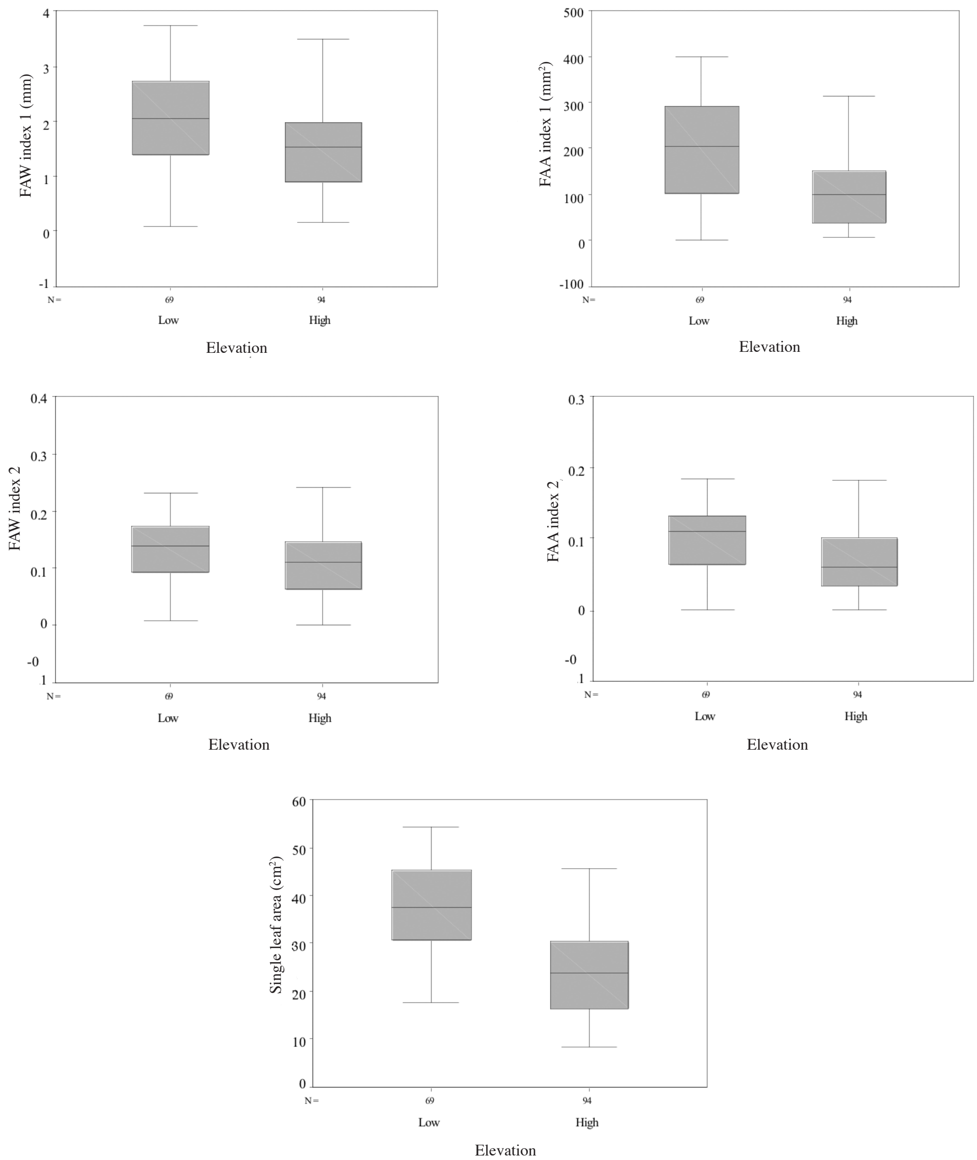

FIGURE 2. Box plots of leaf fluctuating asymmetry and single leaf area of *C. utilis* in forest understorey in low (1500 m) or high elevation (2000 m)

TABLE 3. Mean number of leaf fluctuating asymmetry and single leaf area (± SE) of *C. utilis* in forest understorey in low (1500 m) or high (2000 m) elevation

Leaf traits	Elevation		*t*
	Low	High	
Single leaf area (cm^2)	37.25±1.15	24.06±0.96	8.852**
Specific leaf area (cm^2/g)	211.51±3.69	239.35±6.97	–3.329**
FAW index 1 (mm)	1.985±0.105	1.526±0.077	3.622**
FAA index 1 (mm^2)	203.05±13.32	111.16±8.79	5.757**
FAW index 2	0.134±0.006	0.108±0.005	3.118**
FAA index 2	0.103±0.005	0.071±0.005	4.499**

where FAA is the fluctuating asymmetry based on leaf area, FAW the fluctuating asymmetry based on leaf width. *t* values and significant differences from *t test* are given. * $p<0.05$, ** $p<0.01$

rainfall, moisture, slope and slope location with elevation might be significant for bamboo growth.

Forest canopy condition played an important role in shaping long-term understorey structure and dynamics (Taylor et al. 2004). The effect of canopy condition on bamboo population and plasticity has been studied in other bamboo species, such as *Sasa* (Suzaki et al. 2005) and *Fargesia* (Wang et al. 2012, 2009; Yu et al. 2006). Morphological responses of bamboos to canopy condition are variable, depending on taxa and site conditions. In our study, canopy condition had an obvious effect on morphological plasticity and of *C. utilis*. Forest understorey (canopy density 74–80%) had higher culm height and diameters, height under branch, node number and shoot number than forest edge (20-25%). Canopy cover was an important factor influencing forest understorey conditions such as light, temperature and moisture (Wang et al. 2009). When living in a more shady environment (under higher canopy cover, RPFD <5%), it was difficult for get enough light, which would likely result in lower growth rates and survival (Li et al. 2013; Wang et al. 2012). Most bamboos do not tolerate full shade, resulting in the lowest height and new shoots, with the smallest diameters (Wang et al. 2006). However, under more open canopy conditions (canopy cover <25%), the high light and low water content in forest edge hinder resource utilization, photosynthesis and clonal growth of rhizome of the bamboo stand, resulting in lower growth and development of individuals (Li et al. 2013).

Bamboo faced competition from weeds and shrubs that benefit from sunny conditions and grow better in such habitat and which likely compete with bamboo seedlings for nutrients and water (Holmgren et al. 1997). Our result was similar to the previous findings which show the bamboo growth best regeneration was under a medium canopy cover on *Fargesia nitida* in Wolong Nature Reserve (Yu et al. 2006). The study on arrow bamboo also showed that canopy cover had highly significant effects on bamboo growth, which was highest and showed the best regeneration under medium to medium-high canopy cover (0.41-0.60 and 0.61-0.80) (Li et al. 2013). Plants often exhibited the response of plasticity to light differences in open canopy and shade environments (Osada et al. 2003). Species capable of morphological plasticity were recognized more successful across varying environmental conditions and resource stress, an especially important trait for monocarpic bamboo (Taylor et al. 2004). Bamboos optimized the efficiency of light and water use in their clonal growth by spreading or by morphological plasticity. Shoot number is determined by light when there is an adequate supply of water and nutrients, which indicated forest understorey at high elevation was favor of shoot productivity.

Single leaf area (SLA), absolute fluctuating asymmetry (index 1 of FAW and FAA) and size-scaled fluctuating asymmetry (index 2 of FAW and FAA) were significantly higher in low elevation than in high elevation of forest understorey, which exhibited significant relationship with altitude and indicated environment stress had significant effect on FA and SLA. It was consistent with previous study that leaf fluctuating asymmetry were significantly correlated with altitude along the mountain (Albarrán-Lara et al. 2010; Hagen et al. 2008). Varying climates was recognized to be the main determinants of plant species in the mountain forest. The high variability in FA between elevations could be explained by air temperature, relative air humidity (Hagen et al. 2008), light influenced by slope and slope location. Stress of low elevation might result from high slope (7-15°) and low slope location, along with rainfall and moisture. Thus, FA was a useful and cost efficient monitoring tool for assessing elevation stress and detecting immediate forest responses to climate impacts also in the spatial domain, which is consistent with previous findings on birch and *Quercus* species (Albarrán-Lara et al. 2010; Hagen et al. 2008).

Higher leaf size at low elevation might result from light obtaining and stem or underground competition with other species, which also indicated high environment stress at low elevation. A higher SLA at high elevation was favour of absorption of photosynthetic active radiation to growth (Poorter et al. 2009). The presence of variation in water availability, air temperature and light influenced by slope and slope location are mainly responsible for variation in SLA among leaves.

Our results marginally indicated that high light and low elevation are limiting factors on bamboo growth in the Jinfo Mountains and forest understorey at high elevation favor bamboo growth. Environmental selective forces shaping variation of morphological traits and leaf fluctuating asymmetry of *C. utilis* in contrasting canopy condition and elevations might lead population adaptation to different mountain forest habitats.

ACKNOWLEDGMENTS

This research was supported by the National Natural Science Foundation of China (No. 31000194, 31270465, 31070404) and by the Foundation for Key Youth Teachers of Xuchang University, Henan Province Science and Technology project (122300410005).

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Received: 27 August 2013
Accepted: 5 November 2013