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EFFECTS OF CANOPY CONDITION AND RAMET CLASS ON CLONAL PLASTICITY OF DWARF BAMBOO, *FARGESIA DECURVATA*, IN AN EVERGREEN BROADLEAVED FOREST IN THE JINFO MOUNTAINS, CHINA

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ABSTRACT

Dwarf bamboo, a dominant understory clonal plant in temperate forests, is recognized to be an key factor for forest regeneration. However, none has examined effects of canopy condition and ramet class of connected clonal system. In a field experiment, clonal plasticity in a four-connected ramet system of dwarf bamboo, *Fargesia decurvata* were studied under canopy, small gap, medium gap and large gaps in an evergreen broadleaved forest in the Jinfo Mountains, China. In the ramet system level, morphology traits of *F. decurvata* were significantly highest in the medium gap, and smallest in the canopy. Traits of rhizome, spacer and biomass were significantly higher in the large and medium gap than in the small gap and canopy. Canopy condition had a similarly significant effect on traits of morphology, clonal growth and biomass of each ramet component of *F. decurvata*. Number of leaves, total leaf area and shoot biomass were lower, but number of ramets was significantly higher in distal ramet (D class) than those in other three classes. Number and node length of spacers and total spacer length significantly increased in C-D class from forest canopy to large gap, but there was no significant effects in other classes, as a interactive effects of canopy condition and ramet class on spacer traits. Thus, these results indicated a positive influence of gap size on spacer traits of distal ramets of *F. decurvata*. Therefore, interaction of canopy condition and internal age class of ramet system might lead to population adaptation to environmental differences, which shapes plasticity in traits of morphology, clonal growth and biomass of dwarf bamboo in different forest conditions.

Key words: *Fargesia decurvata*; spacer length; clonal growth; clonal integration; ramet class.

INTRODUCTION

Dwarf bamboo is known that has crucial impacts on forest composition, structure and dynamics for their dominant distribution and understory exclusive density in many temperate forests (Taylor *et al.* 2004, Wang *et al.* 2009, Itô and Hino, 2005, 2007, Ishikawa *et al.* 2014), from open site to dense forest understory habitats. Light, soil water and nutrients are commonly heterogeneous distributed in forest habitats (Shi *et al*. 2015). Forest canopy composition and density affect patterns of resource availability (i.e. light, moist, soil nutrients) on the forest floor, which further influence the growth and dispersal of dwarf bamboo (Taylor *et al.* 2004, Wang *et al.* 2012, Hirobe *et al.* 2015). Many clonal plants can spread horizontally and produce connected ramets to adapt different forest microhabitats (Price and Marshall 1999, Weppler and Stocklin, 2005, Wang *et al.* 2013). Due to the clonal life history, dwarf bamboos may optimize the efficiency of light and water use in growth either by morphological plasticity or by clonal integration. Relationships of gaps and understory bamboo have been studied in temperate forests to understand the response of bamboo taxa to forest regeneration (Taylor and Qin, 1992, Wang *et al.* 2006). The growth of *Bashania fangiana* and *Fargesia nitida* was inhibited in subalpine coniferous forest, while there were higher and denser culms in broadleaved forest and forest gaps due to better resource conditions in southwest China (Noguchi and Yoshida, 2005, Suzaki *et al.* 2005; Taylor *et al.* 2004, Yu *et al.* 2006).

Clonal integration can share resources, such as water, photosynthates and nutrients, among individual ramets (Alpert 1991, 1999, Yu *et al.* 2002) on a site. And growth and morphology of ramets will be controlled by the internal allocation of resources within the integrated plant as a whole (Alpert 1991, 1999). Many studies have focused on this cost–benefit analysis, based on plant performance after severing rhizomes or stolons between mother and daughter ramets (Yu *et al.* 2002, Wang *et al.* 2009, 2016a, b). Guerilla type of bamboo had obviously undergrowth age classes and clonal architecture, which might be influenced by clonal integration between different ramet classes in different canopy conditions. The interaction of canopy condition and ramet class might lead adaptive growth and morphology of ramet population of dwarf bamboo in forest.

The mechanisms that dwarf bamboo adapt to understory forest conditions, such as clonal growth and propagation, morphology and physiology, have been well documented (Wang *et al.* 2006, Yu *et al.* 2006, Tao *et al.* 2008). Generally, clonal growth is highly plastic in response to different environments (Weppler and Stocklin, 2005, Pennings and Callaway, 2000, Wang *et al.* 2011). However, little is known about on clonal plasticity of ramets of dwarf bamboo as being affected by different ramet classes and canopy conditions.

The aim of this study was to better understand the effects of canopy condition and clonal integration between four ramet classes on clonal plasticity (biomass, clonal growth and expansion, and morphology) of widespread dwarf bamboo, *Fargesia decurvata*, in an evergreen broadleaved forest of Jinfo Mountain, Southwest China. Specifically, we aimed to the following questions: (1) Does canopy condition alter the clonal growth and expansion, and morphology of ramet system of *F. decurvata* in evergreen broadleaved forest? (2) Does ramet class (age) affect the clonal growth and expansion, and morphology of *F. decurvata* ? (3) Is there an interaction effect of canopy condition and ramet class on the clonal growth and expansion, and morphology of *F. decurvata*?

Study area: The study site was located in an evergreen broadleaved forest of Jinfo Mountain Nature Reserve (29°00′45″N, 107°08′32″E; 1,450 m a.s.l.) in Chongqing, Southwest China. It belongs to subtropical humid monsoon climate with annual average air temperature of 8.5 °C and annual mean rainfall of 1,286.5 mm. The soil substrate is dark yellow and yellow brown soil (Zhang *et al.* 2011). The forest on the site consists mainly of evergreen broadleaved trees such as *Cyclobalanopsis* sp. and *Lithocarpus glabra*, and sporadic deciduous broadleaved trees such as *Stranvaesia davidiana* and *Carpinus cordata*, and the forest floor is mainly covered with *F. decurvata*.

MATERIALS AND METHODS

Study species: *Fargesia decurvata* J. L. Lu is a rhizomatous plant that is distributed widely in mountain forest conditions of central and southwest China, which is also one of the main foods for the giant panda (*Ailuropoda melanoleuca* David). It can mainly produce both guerrilla form (with few and short spacers) and phalanx form (with long spacers) ramets to expand population by robust amphipodium rhizome system. Following colonization by vegetative ramets, the populations of *F. decurvata* commonly develop in evergreen and deciduous broadleaved forest and forest which consist of a large number of understory patches. Clonal growth by rhizomes is the only way to spread ramets during unflowering period that plays an important role in the maintenance of populations of this species.

Measurements: In this study, canopy gap was defined as an area >10 m^2 without any tree crown >15 m high, a definition following Nakashizuka (1989) and Wang (2006). Classification of gap size was based on our previous data in temperate forest gap. Expanded gaps were measured based on consideration of direct and indirect influence by the canopy opening. Canopy (C), small gap (S, 81.67±8.76 m^2), medium gap (M, 151.33±10.40 m^2), and large gap (L, 317.00±34.77 m^2) were divided by gap area in 100 m × 100 m study site (Table 1). Canopy density in each gap and leaf area index was measured by the LAI-2000 Plant Canopy Analyzer (LI-COR, Lincoln, USA) set up above shrub layer in the middle of each gap.

Measurement was mainly conducted in above four canopy types of an evergreen broadleaved forest at flat topography in late August 2011. Each canopy type was composed of eight quadrats of 2 m × 2 m, in which the density of *F. decurvata* was measured. A sample in center of each canopy type included four class ramets from proximal (relatively old, A class) ramet to distal (relatively young, D class) ramet, interconnected by a rhizome (Fig. 1). Eight samples were selected for each canopy type. Measurements included characteristics of clonal growth and expansion (number of ramets, number of spacers, total rhizome length, total spacer length, node length of spacer and number of nodes), morphology (ramet height, ramet base diameter, average node length, number of leaves, total leaf area and specific leaf area), and ramet biomass and allocation (whole ramet, shoot, root, rhizome, spacer and shoot-root ratio). The plants were harvested and then separated into roots, rhizomes, spacers, culms and leaves. Images of leaves of each ramet and spacer were obtained and total leaf area was measured using WinRHIZO Pro v.2004c Root Analysis System (Regent, Canada). Above-ground parts (shoot parts) included culms and leaves, while below-ground parts included roots, rhizomes and spacers. We measured total rhizome length and spacer length (defined as the rhizome length between two adjacent ramets) with a ruler, and measured average node length of spacer (average value of the adaxial and abaxial direct) using Image-Pro Plus Version 6.0 (Media Cybernetics, USA) (Fig. 1). All plant portions were dried at 80 °C for 48 h and weighed.

Data analysis: We employed two-way for effect of canopy condition (canopy, small gap, medium gap, and large gap) and age class (A, B, C and D) of connected ramet system on clonal plasticity. We also used one-way ANOVA for effect of canopy condition on characteristics of clonal growth and expansion, morphology, and ramet biomass and allocation of each ramet class and whole clones separately. If necessary, the data (including percentage 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 among four treatments. Differences were considered significant at $p < 0.05$ level. SPSS statistical package was used for all analyses (SPSS 11 Copyright:

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RESULTS

Clonal plasticity of ramet system in different canopy conditions: Gap size significantly decreased, canopy density and leaf area index significantly increased from large gaps to forest canopy (Table 1).

At the level of ramet system (total four ramet classes), average height, average basal diameter, average node length and total leaf area of *F. decurvata* were significantly highest in the medium gap, and smallest in the canopy (p<0.01). Specific leaf area increased from large gap to canopy (p<0.01) (Table 2).

Ramet density significantly tended to increase, while total spacer length tended to decease from large gap to canopy (p<0.01) (Table 2). Total rhizome length and number of spacers were significantly higher in three type gaps than under canopy (p<0.05). Average node length of spacer and total number of nodes were significantly higher in the large and medium gap than in the small gap and canopy (p<0.01).

Biomass of whole ramets and shoot (aboveground) were significantly highest in the medium gap, and smallest in the canopy (p<0.01). Biomass of root and rhizome were significantly higher in the large and medium gap than in the small gap and canopy (p<0.01). Biomass of spacer significantly tended to decease from large gap to canopy (p<0.01) (Table 2). Shoot-root ratio was significantly highest in the medium gap (p<0.05).

Clonal plasticity of different ramet classes in different canopy conditions: The canopy condition had a highly significant effect on most traits of morphology, clonal growth and biomass of each ramet component of *F. decurvata* (p<0.01) (Table 2). Ramet height, basal diameter of ramet and average node length were significantly highest in the medium gap and smallest under the canopy, and specific leaf area increased with canopy density regardless of ramet class (p<0.05). Total leaf area was tended to highest in the medium gap and lowest under the canopy for three old classes of ramet, while it decreased with canopy density for new ramet (p<0.05) (Fig. 2). Number of spacers, total rhizome length, total spacer length, node length of spacer and number of nodes was decreased from large gap to canopy regardless of ramet class (p<0.05) (Fig. 3). The biomass of each component was decreasing from large gap to forest understory (p < 0.05) (Fig. 4).

Ramet class was significant for number of leaves, total leaf area, number of ramets and shoot biomass (p < 0.05) (Table 2). Number of leaves, total leaf area and shoot biomass in new ramet (D class) were lower than those in other three classes (Fig. 3, 4). Number of ramets in was significantly higher in D ramet class than in A and B class (Fig. 3).

However, number and node length of spacers and total spacer length significantly increased in C-D class from forest canopy to large gap, but there was no significant effects in other classes, as a interactive effects of canopy condition and ramet class on spacer traits (p < 0.05, Table 2, Fig. 4). Interaction between canopy condition and ramet class indicated a positive influence of gap size on spacer traits of new ramets (D class) in *F. decurvata*.

Table 1. The different canopy conditions in an evergreen broadleaved forest in the Jinfo Mountain.

Community characters	Canopy types				F
	L	M	S	C	
Size of expanded gap (m^2)	317.0±34.8	151.3±10.4	81. 7±8.8	/	38.70**
Canopy density (%)	61.5±2.6	75.4±2.3	84.0±2.1	92.2±1.0	39.62**
Leaf area index	1.6±0.1	2.5±0.2	3.3±0.2	4.1±0.2	52.07**

L: Large gap; M: Medium gap; S: Small gap; C: Canopy. The same below. F values and significant differences from one-way ANOVAs are given. * P < 0.05, ** P < 0.01.

Table 2. Morphology, clonal growth and expansion, ramet biomass of *F. decurvata* ramet system (total four ramet classes) in different canopy conditions in field experiment of an evergreen broadleaved forest.

Plant traits	Canopy conditions				F
	L	M	S	C	
Morphology					
Average height (cm)	109.8±6.1	143.4±9.3	95.4±1.4	77.3±6.6	19.30**
Average basal diameter (mm)	4.73±0.07	5.43±0.15	4.04±0.21	3.28±0.26	21.76**
Average node length (cm)	8.11±0.42	10.50±0.37	8.20±0.62	6.48±0.75	7.71**
Total leaf area (m^2)	2212±262	3792±812	1340±157	912±219	10.54**
Specific leaf area (m^2/g)	167.1±1.9	150.9±3.1	173.7±4.8	195.5±6.2	18.39**
Clonal growth and expansion					
Ramet density (no./m^2)	6.50±0.69	7.60±0.84	12.50±0.81	17.00±1.02	45.10**

Total rhizome length (cm)	39.85±2.77	37.07±2.23	33.88±8.34	16.14±3.66	4.39*
Number of spacers	7.25±0.25	5.67±0.33	6.25±0.63	3.75±0.25	13.79**
Total spacer length (cm)	128.38±6.77	96.50±2.75	61.13±3.06	48.60±10.20	28.91**
Average node length of spacer (cm)	0.80±0.01	0.75±0.01	0.63±0.01	0.62±0.01	59.95**
Total number of nodes	125.38±7.41	126.00±8.39	82.00±5.91	65.88±9.65	14.70**
Biomass (g)					
Whole ramets	62.04±2.39	95.29±6.78	38.58±2.31	19.65±4.64	26.19**
Shoot (aboveground)	43.20±3.82	75.93±6.05	25.86±1.44	14.03±3.86	21.43**
Root	19.15±1.80	19.36±1.90	11.51±1.35	5.63±1.04	19.02**
Rhizome	7.12±0.53	8.15±1.29	4.80±0.56	2.33±0.44	13.82**
Spacer	10.16±1.66	8.26±0.50	4.51±0.75	1.99±0.77	11.90**
Shoot-root ratio	2.37±0.41	3.89±0.31	2.33±0.30	2.16±0.28	4.92*

F values and significant differences from one-way ANOVAs are given. * $P < 0.05$, ** $P < 0.01$.

Table 3. ANOVA summary of the effect of canopy condition, ramet class, and interaction on ramet biomass (whole ramet, aboveground part (shoot), belowground part (root), rhizome, spacer and shoot/root ratio), clonal growth and expansion (number of ramets, number of spacers, total rhizome length, total spacer length, node length of spacer and number of nodes) and morphology (ramet height, ramet base diameter, average node length, number of leaves, total leaf area and specific leaf area) of *F. decurvata* in field experiment of an evergreen broadleaved forest

Morphology	**DF**	**Ramet height**	**Basal diameter of ramet**	**Average node length**	**Number of leaves**	**Total leaf area**	**Specific leaf area**
Canopy condition	3	**27.90*** **	**30.67*** **	**12.43*** **	1.73	**12.40*** **	**28.75*** **
Ramet class #	3	2.18	2.88	0.80	**3.47***	**3.34***	0.29
Canopy × Class	9	0.86	0.96	0.85	0.93	1.53	2.16
Whole Model	15	**6.45*** **	**7.39*** **	**3.19*** **	1.42	**3.91*** **	**16.52*** **
Clonal growth	DF	Number of ramets	Number of spacers	Total rhizome length	Total spacer length	Node length of spacer	Number of nodes
Canopy condition	3	2.01	**4.39** **	**10.85*** **	**18.02*** **	**58.33*** **	**13.61*** **
Ramet class #	3	**22.13*** **	0.45	0.98	3.20	1.28	0.36
Canopy × Class	9	0.97	**2.19***	0.98	**3.48** **	**11.48*** **	0.55
Whole Model	15	**5.41*** **	**2.29***	**3.00** **	**7.51*** **	**24.68*** **	**4.09** **
Biomass	DF	Whole ramet	Shoot	Root	Rhizome	Spacer	Shoot/root ratio
Canopy condition	3	**28.91*** **	**25.01*** **	**28.70*** **	**16.86*** **	**21.02*** **	1.87
Ramet class	3	1.47	**3.86***	0.35	0.22	0.70	0.86
Canopy × Class	9	1.31	1.45	1.81	1.44	1.17	1.88
Whole Model	15	**6.80*** **	**6.31*** **	**6.91*** **	**4.28*** **	**5.08*** **	1.63

Parameters related to spacer only have three ramet classes (d.f.= 2, 6 and 12 for ramets class, canopy × class and whole model, respectively), another parameters have four ramet classes. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$

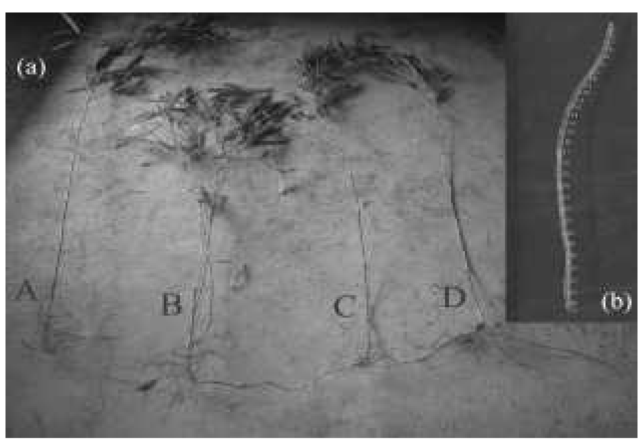

Fig. 1. Sample of four ramet classes (a) and measurement to average node length of spacer (b) of dwarf bamboo, *F. decurvata* in a middle gap of the evergreen broadleaved forest, Jinfo Mountain, southwest China. A, B, C and D represent four ramet classes that from proximal (relatively old) ramet to distal (relatively young, 1yr old) ramet.

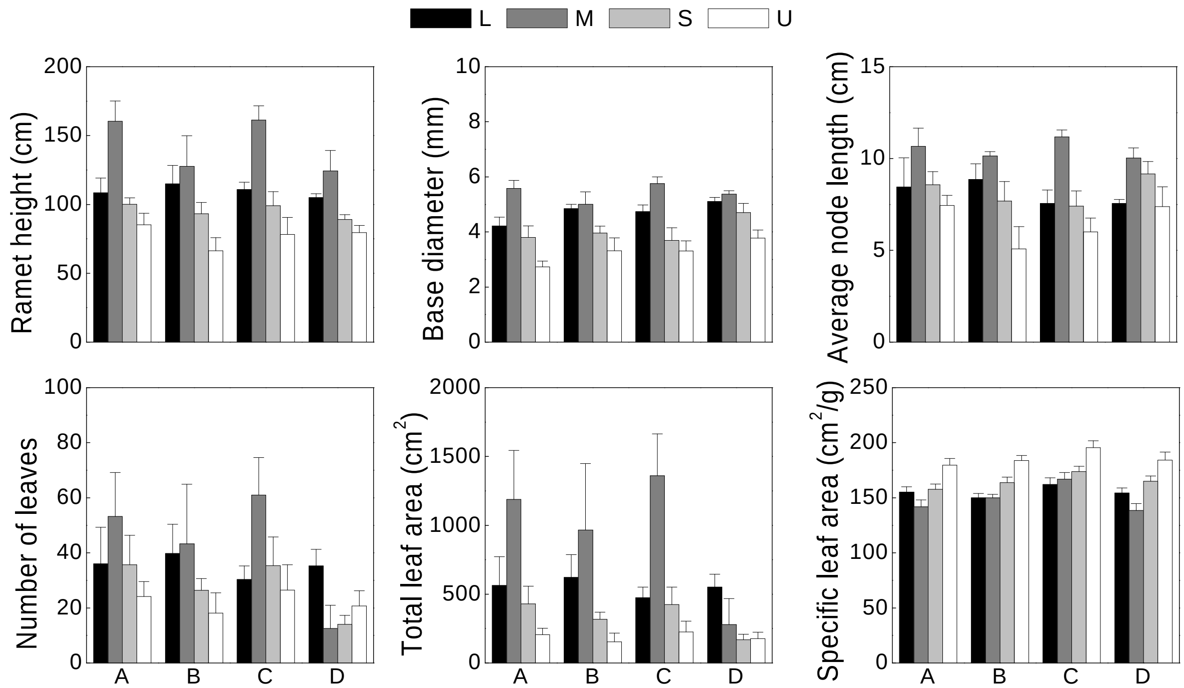

Fig. 2. Morphology (ramet height, ramet base diameter, average node length, number of leaves, total leaf area and specific leaf area) of *F. decurvata* in different canopy conditions for four ramet classes in field experiment of an evergreen broadleaved forest. A, B, C and D represent four ramet classes that from proximal (relatively old) ramet to distal (relatively young, 1yr old) ramet. L: Large gap; M: Medium gap; S: Small gap; C: Canopy. The same below.

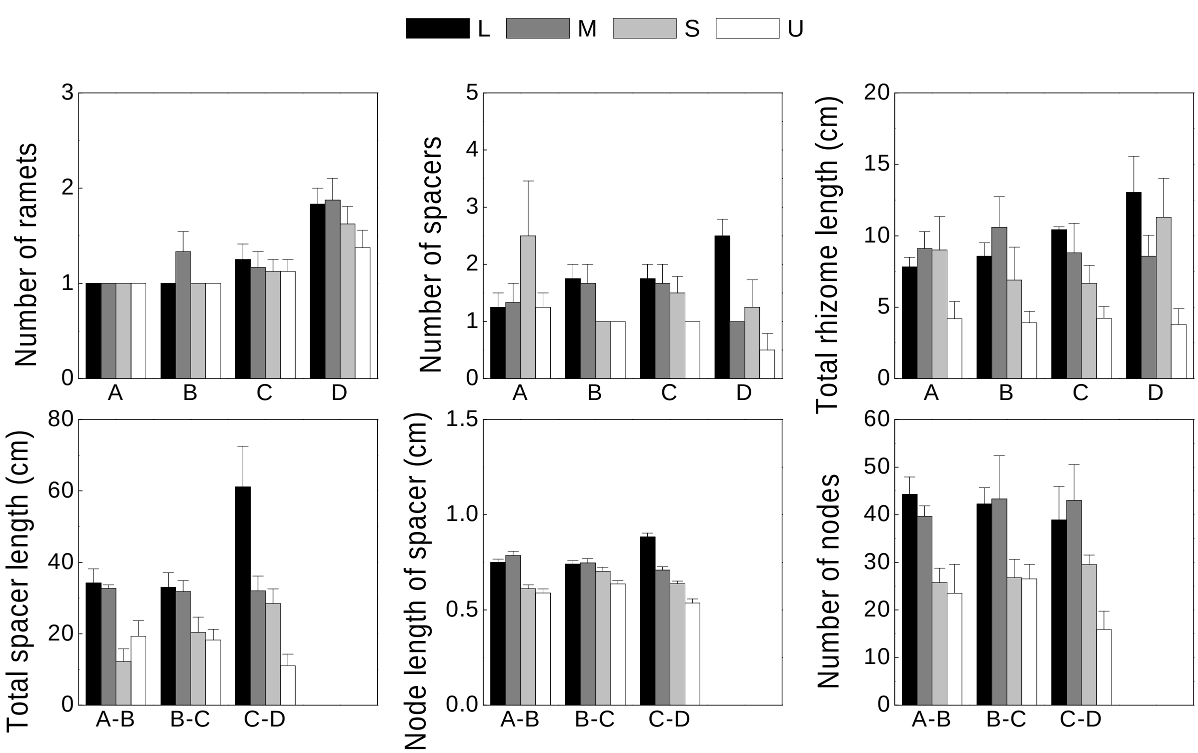

Fig. 3. Clonal growth and expansion (number of ramets, number of spacers, total rhizome length, total spacer length, node length of spacer and number of nodes) of *F. decurvata* in different canopy conditions for four ramet classes in field experiment of an evergreen broadleaved forest

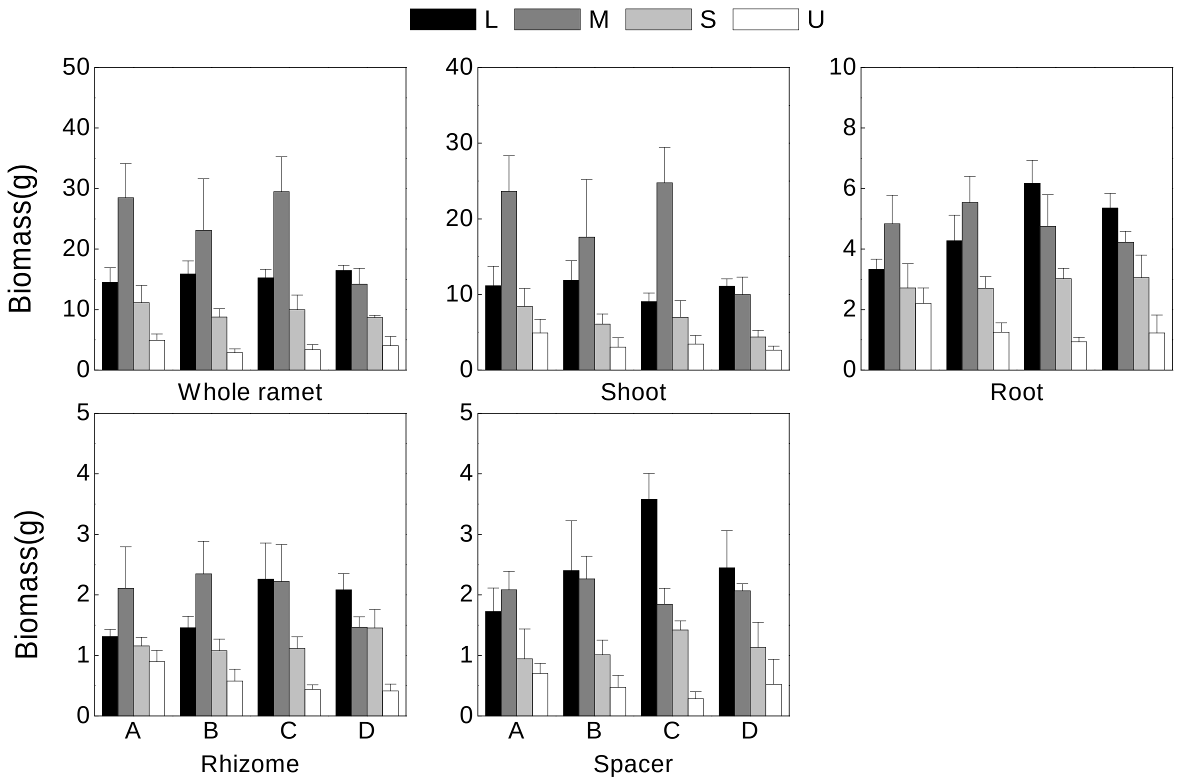

Fig. 4. Ramet biomass (whole ramet, shoot, root, rhizome, spacer and shoot-root ratio) of *F. decurvata* in different canopy conditions for four ramet classes in field experiment of an evergreen broadleaved forest. A, B, C and D represent four ramet classes that from proximal (relatively old) ramet to distal (relatively young, 1yr old) ramet.

DISCUSSION

While many studies have tested effects of canopy condition on growth, morphology and clonal plasticity of dwarf bamboo in temperate forest (Wang *et al.* 2006, Noguchi and Yoshida 2005, Suzaki *et al.* 2005; Yu *et al.* 2006, Tao *et al.* 2008), none has examined those effects on a connected ramet system of dwarf bamboo with distinct age class. The results confirmed both canopy condition and ramet class significantly affected on most traits of clonal plasticity of *F. decurvata*. Traits of morphology, clonal growth and biomass of each component in the large or medium gap were higher than those under forest canopy, which implied that bigger gaps might be optimal where the moisture and temperature conditions are most favorable for bamboo regeneration (Wang *et al.* 2009, Li *et al.* 2014). Forest canopy condition, influencing forest understory conditions such as light, temperature, and moisture, played an important role in shaping long-term understory structure and dynamics (Wang *et al.* 2009, Noguchi and Yoshida, 2005). Climatic conditions (temperature and moisture) changed, to some extent, rainfall and slope location varied from gap to forest understory, resulting in different micro-climate habitats (Li *et al.* 2014, Whitmore 1989).The effect of gaps on bamboo population and plasticity has been studied in other bamboo species, such as *Chusquea foliosa* (Widmer 1998), and *Sasa* species (Kawahara 1987), *F. nitida* (Tao *et al.* 2008) and *F. qinlingensis* (Wang *et al.* 2006). 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 lower survival (Wang *et al.* 2012; Li *et al.* 2013). In this study, gaps had an obviously positive effect on morphology, clonal growth and biomass in both ramet system and ramet level of *F. decurvata*. Parameters showed that large gaps had higher rhizome and spacer traits, and biomass. One explanation is that increased light with sufficient water content led to photosynthates accumulation and quick growth of the bamboo ramets (Wang *et al.* 2006), resulting in higher morphological traits (i.e. ramet height, basal diameter, node length, and total leaf area), clonal growth (such as ramet density, total rhizome length, number of spacers, total spacer length, node length of spacer) and biomass of whole ramets, shoot, root, rhizome and spacer. Bamboos commonly shows plastically response to light differences in gap and shade environments (Wang *et al.* 2006). Furthermore, bamboo species, be monocarpic and flowering at long intervals, capable of architectural plasticity that are considered more successful across varying environmental conditions (Yu *et al.* 2006, Tao *et al.* 2008). Therefore, bamboos optimize the efficiency of light availability in their clonal growth by spreading (Whitmore 1989) or by morphological plasticity (Widmer 1998). The above data suggest light is a limiting factor on bamboo growth in the Jinfo Mountains, and gaps favor bamboo growth. A integrative habitats of rainfall, moisture, slope and slope location with elevation might be significant for bamboo growth.

Ramet class had significantly effect on number of leaves, total leaf area, number of ramets and shoot biomass. The explanation is that increased ramet age led to higher photosynthates and growth of the bamboo ramets. So number of leaves, total leaf area and shoot biomass in distal ramet (D class) were lower. However, distal ramet (D class) had higher shooting ability than other age classes.

However, our results indicated a positive influence of gap size on spacer traits of distal ramets of *F. decurvata*. Rapid growth of spacer (i.e. rhizome) might lead to the higher ability of growth and shooting in new ramets. Clonal growth and expansion of bamboo in different canopy conditions depends on the adaptation in ability of rhizome elongation. ramets with longer and larger rhizome had higher activity in resource transportation and survival rate, thus achieved faster growth in many bamboo species (Wang *et al.* 2006, 2009, Yu *et al.* 2006). This was consistent with the hypothesis that larger rhizome will accumulate more storages (nutrients, carbohydrate and hormonal content) to stimulate plant and growth. Furthermore, sharing of resources between connected ramets could increase the performance of clonal plants when ramets experience resource availabilities in different canopy conditions (Hutchings and John, 2004, Roiloa and Retuerto, 2007, Alpert *et al.* 2002, Alpert 1999, Dong 1993). In the relatively resource-rich conditions (such as large and medium gaps), resources might be easily transported from proximal ramets to distal ramets. Then integration could increase performance of distal ramets and the whole ramet system. The findings further supported the source-sink hypothesis, suggesting that differences in resource uptake between old and new ramets drive the sharing process, with resources moving from ramets with high uptake ability or favorable resource to resources to those with low uptake ability or unfavorable resource by clonal integration (Alpert 1999, Dong 1993, He *et al.* 2010, Guo *et al.* 2011, Wang *et al.* 2016a, b).

Conclusions: Our results indicated that canopy condition and ramet class of connencted clonal system are key factors on growth of *F. decurvata* in the Jinfo Mountains, and distal ramets in connected ramet system show greater response of clonal organ (spacer or rhizome) to gap sizes. And there is a positive influence of gap size on spacer traits of distal ramets. Therefore, interaction of canopy condition and internal age class of ramet system might lead to population adaptation to environmental differences, which shapes plasticity in traits of morphology, clonal growth and biomass of dwarf bamboo in different forest conditions.

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Authors' contributions: Chang-Gen Lin, Zhen Li and Ai-Ming Cai conducted experiments, Chang-Gen Lin, Ai-Ming Cai and Yong-Jian Wang wrote the paper. Yong-Jian Wang designed the experiment, Ping Zhang, Lie Xu and Rong Yan contributed to data analysis and provided assistance during experiments.

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

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