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Ramet population structure of *Fargesia nitida* in different canopy conditions of the subalpine dark coniferous forest in the Wolong Nature Reserve, China

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Abstract The bamboo *Fargesia nitida*, one of the giant panda's main food sources and the dominant shrub species of the forest understory, is mainly distributed in the dark coniferous belt in western Sichuan and southern Gansu in China. To study the impact of different forest canopy conditions on subalpine dwarf bamboo populations, ramet population structures of clonal *Fargesia nitida* were surveyed in: forest understory (FU), moderate gap (MG), large gap (LG) and marginal open space (MOS). In order to determine how the ramet structures could be affected and its effects on these four canopy conditions, a field survey of the age structure of *Fargesia nitida* population, its morphological traits and biomass was conducted in the *Abies faxoniana* forest situated in the Wolong Nature Reserve, western Sichuan, China. The main results were as follows. First, at the ramet level, the structures of the ramet populations in four canopy conditions were significantly different, and as the canopy density decreased, the mean height, basal diameter and biomass of the populations increased following the order: LG < MG < FU. Second, the biomass proportions of ramets modularly varied with different canopy conditions and leaf biomass proportion was positively related to the canopy density except for the MOS where the biomass proportions of rhizome and roots were both higher than those in the three other canopy conditions. Third, ramet specific leaf weight increased in parallel with the decrease in canopy density. In the MG, the values of the individual leaf biomass and leaf area were the largest, followed by those in the MOS. Both the individual leaf biomass and leaf area were significantly different from those in the FU and LG. Leaf number per ramet

was significantly different among the four different canopy conditions and the biggest in the LG. Fourth, the ramet population mortality was the lowest in the FU (Chi-square test, $p < 0.01$), while there was no significant difference in the average population age (Mann-Whitney test, $p > 0.05$). All the results indicated that it was not ramet age, but the morphological changes and biomass distribution that exhibited the response of the ramet population of *Fargesia nitida* to the changed canopy conditions.

Keywords *Fargesia nitida*, ramet population, population structure, subalpine dark coniferous forest, Wolong Nature Reserve

1 Introduction

Forest gap regeneration is a main way of regeneration in subalpine dark coniferous forests (Liu et al., 2001; Wang et al., 2004). The gap provides a favorable living condition for subalpine dwarf bamboos, the dominant species in the forest understory. The dwarf bamboo can invade the gap and finish clonal propagation rapidly, so it can affect the growth of seedlings and tree regeneration and greatly reduce the tree species biodiversity of forests (Editorial Board of Forests in Sichuan, 1992; Qin et al., 1993; Taylor et al., 1995, 1996; Hiura et al., 1996). To some extent, the existence of dwarf bamboo is considered as a key factor influencing the seedling regeneration of arbor tree in gaps (Qin et al., 1993; Qi et al., 2004). Therefore, studies on the growth and annidation of dwarf bamboos, and its effect on the gap regeneration and gap dynamic change in the subalpine dark coniferous forest, are important for further research on forest regeneration (Qi et al., 2004).

Up to now, research on dwarf bamboos only focused on the age structure, biomass and propagation of the population in a MOS bamboo species (Qin et al., 1993; Wang and Ma, 1993). Some relative studies showed that the growth of dwarf bamboo is different in different canopy conditions in

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the subalpine coniferous forest (Qin et al., 1993; Wang and Ma, 1993; Qi et al., 2004). Less is known about the clonal ramet population structure, dynamic change and its adaptation to different canopy conditions. In this paper, we try to understand: 1) in the ramet level, whether there is difference of performance structures and age structures of *Fargesia nitida* in different canopy conditions; and 2) if a difference exists, what the relationship between these differences and their living canopy conditions is.

2 Studied site

This study was carried out at the Wolong Subalpine Dark Coniferous Forest Ecosystem Research Station (102°58'21"N, 30°51'41"E, elevation of 2,800 m) in the Wolong Nature Reserve, Sichuan Province, China. It is a transitional area from the Sichuan Basin to the Qingzang (Tibetan) Plateau. Climate in this region is Qingzang plateau climate (Qin et al., 1993; Li et al., 2004), cool and small annual temperature difference, distinctive dry and wet seasons, relative high humidity with the annual average temperature of 4.3°C, precipitation 848.9 mm, and sunshine duration of 1,185.4 h. The soil is mountain dark-brown coniferous soil (Li et al., 2004).

3 Materials and methods

3.1 Plant materials

F. nitida is a dwarf bamboo and a food source of the giant panda. It is a perennial but monocarpic after 50–60 year woody clonal plant. Gregarious plants, 2–5 m in height and 1–2 cm in diameter, form a fasciculate ramet group or near scattered ramet distribution. Its clonal growth depends on rhizomatous expansion belonging to the phalanx type. It is distributed in southern Gansu Province and western Sichuan Province, China (Qin et al., 1993; Flora of China Editor Commission, 1996).

3.2 Field experiment

Field experiment was carried out in the understory and forest edge at the same elevation ($2,800 \pm 25$) m, slope degree and exposure in the subalpine dark coniferous forest. Based on the investigation of the gap area distribution in 2003, the medium gap (158.3 m²), large gap (401.2 m²), understory and forest edge (bamboo forest, > 1,500 m²) were set as sample plots. Eight 4 m × 4 m quadrates were selected in each plot, and the ramet number and clump number were counted. One hundred ramets were randomly selected to measure their ages, heights and basal diameters. Twenty ramets of the 40 labeled ramets were chosen to measure leaf number, individual leaf area and leaf mass. The remaining 20 ramets were divided into six

parts: the thick root, the fine root, the rhizome, the stem, the branch, and the leaf for the ramet traits investigation, and were then dried for 72 h to obtain the dry mass.

3.3 Data analysis

Based on the height in four canopy conditions, ramets were divided into four classes: I: <2 m, II: 2–3 m, III: 3–4 m and IV: ≥4 m; basal diameter was also grouped into five classes: I: <0.5 cm, II: 0.5–0.9 cm, III: 1.0–1.2 cm, IV: 1.3–1.4 cm and V: ≥1.4 cm; based on growth traits and function difference, roots were classified into the thick root (diameter >0.5 cm) and the fine root (diameter <0.5 cm); according to the age distribution, ramet population was divided into four age classes: I: 1–3 year (in juvenile stage), II: 4–6 year (in adult stage), III: 7–9 year (in senile stage) and IV: >9 year (approaching to death).

Data of ramet height, basal diameter, biomass and leaf parameters were analyzed by using one-way ANOVA and LSD. The death rate between different ramet populations was compared by Chi-square test. Mann-Whitney test was used to test the difference in the average age in different populations. All the data analysis was accomplished in SPSS 11.0.

4 Results

4.1 The height class structure of ramet population

In the marginal open space (MOS), all the four height classes of ramet population were distributed, and there were only three height classes in the other three canopy conditions (Fig. 1a). The ramets of height classes I and II were distributed mostly in the forest understory (FU) accounting for 84% of the total number of ramets. There were more ramets distribution of classes II and III in both the moderate gap (MG) and the MOS accounting for 86% and 85%, respectively. The ramets of height classes III and IV were dominant in the large gap (LG) accounting for 88%. In the order of FU → MOS → MG → LG, the number of ramets decreased in classes I and II, and increased in classes III and IV. The mean height in different canopy conditions were: FU (2.34 m) < MOS (3.03 m) < MG (3.29 m) < LG (3.72 m) and in different canopy conditions were significantly different (ANOVA (analysis of variation), $p < 0.01$) (Fig. 1b).

4.2 The diameter class structure of ramet population

In the FU, the number of ramet in diameter classes II and III accounted for 82% of the total ramets. In the MG and the MOS, the number of ramet in diameter classes III and IV accounted for 67% and 68%, respectively. In the LG, the ramet in diameter classes IV and V accounted for 76%. In the order of FU → MOS → MG → LG, the number of ramets decreased in classes II and increased in classes IV and V (Fig. 2a). In the four canopy conditions, the order of mean diameter given were as follows: FU (0.902 cm) < MG

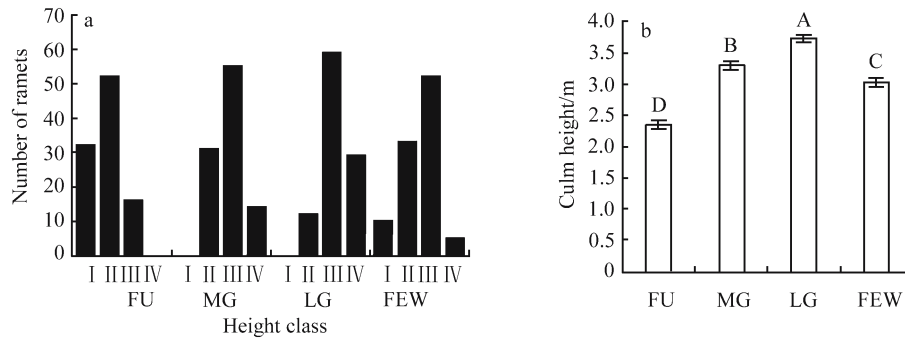


Fig. 1 Ramet-height distribution

(a) The mean value (\pm SE) of plant height; (b) *Fargesia nitida* populations in different canopy conditions.

Note: The values sharing the different letters are significant different at $p < 0.05$; FU: forest understory; MG: moderate gap; LG: large gap; MOS: marginal open space.

(1.202 cm) < MOS (1.228 cm) < LG (1.310 cm) (Fig. 2b). The results of ANOVA and LSD showed that there was significant difference (ANOVA, $p < 0.01$) between mean diameter besides the MG and the MOS.

4.3 The biomass allocation of ramet population

In the order of FU \rightarrow MOS \rightarrow MG \rightarrow LG, the biomass of stem increased, all over 50%. The biomass percentage of leaf

was the biggest in the FU, and it decreased in the order of FU \rightarrow MG \rightarrow LG. The biomass percentages of rhizome, thick root and fine root were all the biggest in the MOS (Fig. 3a). In the four canopy conditions, the order of the mean values of biomass given as follows: FU (41.879 cm) < MG (103.410 cm) < MOS (121.834 cm) < LG (168.914 cm) (Fig. 3b). The results of ANOVA and LSD revealed that there was significant difference in biomass of ramet population among the four conditions.

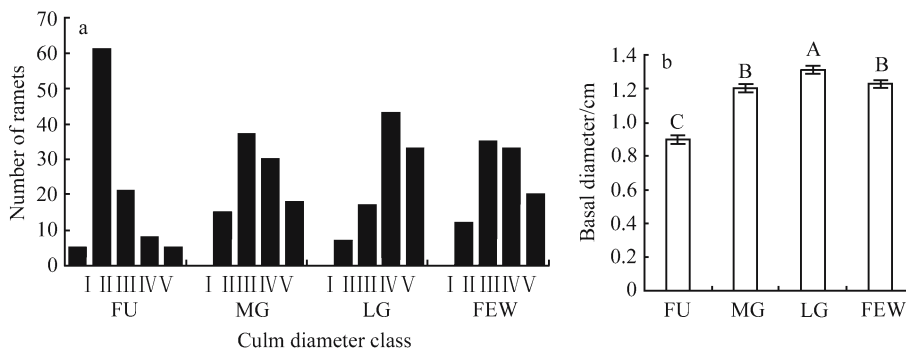


Fig. 2 Ramet-basal diameter distribution

(a) The mean values (\pm SE) of basal diameter; (b) *Bashani fangiana* populations in different canopy conditions.

Note: The values sharing the different letters are significant different at $p < 0.05$. The meaning of the FU, MG, LG, MOS are the same as Fig. 1.

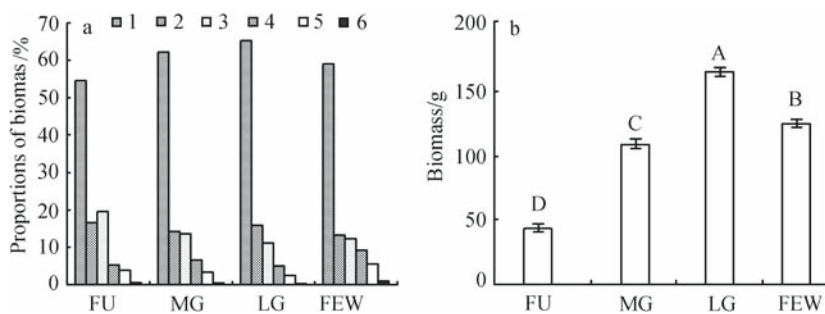


Fig. 3 Biomass allocation proportion

(a) The mean values (\pm SE) of biomass; (b) *Bashani fangiana* populations in different canopy conditions.

Note: The values sharing the different letters are significant different at $p < 0.05$; the letter FU, MG, LG, MOS are the same as Fig. 1. 1: stem; 2: branch; 3: leaf; 4: rhizome; 5: thick root; 6: fine root

4.4 Leaf parameters

The specific leaf weight (mg/cm^2) decreased in parallel with the decrease in canopy density: MOS (3.42) > LG (3.28) > MG (3.13) > FU (2.99), and there were significant differences among all populations (ANOVA, $p < 0.05$) (Fig. 4a). The individual leaf biomass decreased following the order: MG (18.20 mg) > MOS (17.40 mg) > LG (13.35 mg) and FU (13.00 mg), and there were significant differences between the MG and the MOS and between the LG and the MOS (ANOVA, $p < 0.05$) (Fig. 4b). In the MG, the individual leaf area was the largest, followed by that in the MOS. There were significant difference (ANOVA, $p < 0.05$) in individual leaf area between the MG and the MOS. (Fig. 4c). Leaf number per ramet in the LG was the biggest and significantly larger than the other three populations (ANOVA, $p < 0.01$).

4.5 Traits of age structure

The number of ramets distributing in class I and II accounted for 56% in the FU, 71% in the MG, 63% in the LG and 70% in the MOS of the total ramets (Fig. 5). After the standardization of the ramet number of age class, we got the mortality of different populations, 43.9% in the FU, 49.5% in the MG, 50.5% in the LG and 49.1% in the MOS. It was found that there were significant differences in the mortalities of the FU and the other three canopy conditions (Chi-square test, $df = 3$, $\chi^2 = 30.548$, $p < 0.01$), but there were no significant difference among the other three populations (Chi-square test, $df = 2$, $\chi^2 = 4.249$, $p = 0.120$). The weighted average

ages of random statistical individuals were 4.85 ± 0.59 years in the FU, 4.19 ± 0.61 years in the MG, 4.14 ± 0.56 years in the LG and 4.14 ± 0.58 years in the MOS. In the FU, the mean age was bigger than the other environmental conditions, but there was no significant difference among the four environmental conditions (Mann-Whitney test, $U = 4,309.5$, 4,337.5, 4,303.0, 4,921.5, 4,976.0, 4,972.5, $df = 1$, $p > 0.05$).

5 Discussion

The differences in the availability of light under different forest canopy conditions caused the differences in the growth of the species (Tabarelli and Mantovani, 2000). Canopy density (light intensity) influenced the growth and generation of bamboos (Wang and Ma, 1993; Tabarelli and Mantovani, 2000). Studies on *Chusquea* spp. by Widmer (1998) showed that the number and diameter class of *Chusquea* spp. increased from the forest understory to the gap condition. It was similar to the results in our study, under the subalpine coniferous forest canopy, the degree of decentralization increased and the number of ramets and the diameter class of *F. nitida* decreased from the LG, MG to FU. The number of ramets in each sample bundle and density were higher in the LG than those in the other conditions. Studies on lianas and clonal plants have indicated that plant height of *Gynostemma pentaphyllum* increased with the decrease in light (He and Zhong, 2000), and biomass of *Lysimachia congestiflora* decreased with the decrease in light (Chen et al., 2004). Plant height of *Fargesia nitida* population was not the highest in

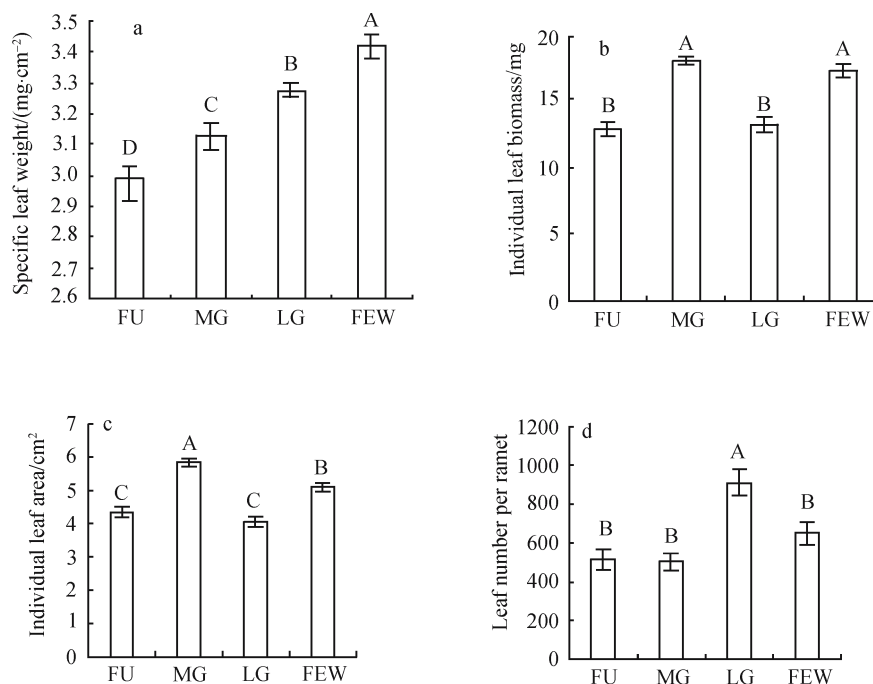


Fig. 4 Leaf parameters in different canopy environment conditions (mean and SE)

Note: The values sharing the different letters are significant different at $p < 0.05$; the meanings of the FU, MG, LG, MOS are the same as Fig. 1.

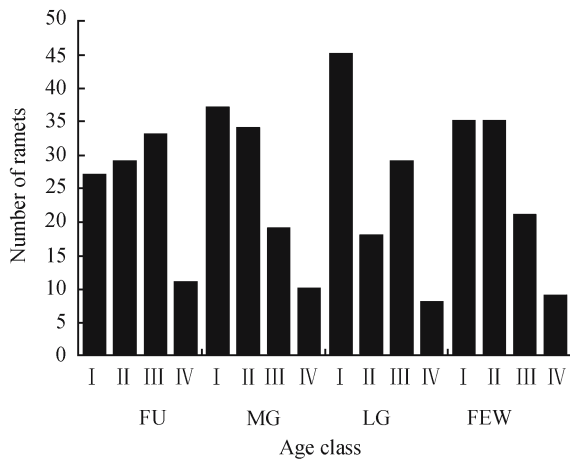


Fig. 5 Ramet-age distribution of *Fargesia nitida* populations in different canopy conditions

Note: The meaning of the FU, MG, LG, EW are the same as Fig. 1.

the FU and the biomass of *F. nitida* was not the largest in the MOS in our study, but showed that different plants had differences in performance and survival strategy with the change of light. The climate condition (heat and water content) was the main factor that determined the distribution and healthy growth of bamboos in the horizontal and vertical scales (Qin et al., 1993; Wang and Ma, 1993). Comparison of the performance structure of *F. nitida* in different forest canopy conditions could reveal the intensity that environmental factors that affected *F. nitida* and that *F. nitida* adapted to the environment (Zhang et al., 2004). The LG was suitable for *F. nitida* (Qin et al., 1993) because light intensity in it was higher than that in the MG and FU, and water content in it was more abundant than that in the MOS. Growth of *F. nitida* was best in the LG of the subalpine coniferous forest, which was similar to those characteristics that plants can fully make use of the light, temperature, water and soil conditions in suitable conditions to extend their survival best (Zhang et al., 2004).

Studies on the resource allocation of the clone spacer of *Pleioblastus maculate* found that resource invested in clone growth of the underground part in low water content condition (Liu et al., 2004). Biomass percentages of ramets and roots, and length of rhizome and thick roots, were all the highest, and the number of fine roots was the largest in the MOS, which was correlated with high light intensity and low soil and atmospheric humidity in the MOS. Long rhizome and lots of fine roots meant *F. nitida*'s strong extend potentials and water intake capacity and compensates for the decrease of water availability. Those could be considered as a foraging behavior of clonal plants (bamboos) for water resources (Liu et al., 2004) and an effective ecological strategy to get more resources in disadvantageous environment (de Kroon and Schieving, 1991; Zhong, 1995).

Leaf biomass percentages decreased from the FU, MG to LG, and the specific leaf weight is: MOS > LG > MG > FU.

The biomass of *F. nitida* is focused on the photosynthesis organ-leaf construction in the FU because of low light intensity, simultaneously, was caught by mean of investment that decreasing specific leaf weight to adapt to low light intensity (He and Zhong, 2000; Zhang et al., 2002). The individual leaf area of plants increased and the leaf number per ramet decreased with the decrease of light intensity in some studies (Li et al., 1995; He and Zhong, 2000). However, the individual leaf area was the biggest in the MG, followed by the MOS (Fig. 4c), which was associated with obviously favorable light in the MG that *F. nitida* made use of it to improve the utilization of resources and production capacity. The individual leaf area of the LG was smaller than that of the MOS, which was correlated with higher leaf number per ramet in the LG (Fig. 4d).

Studies on *Bashania spanostachya* by Wei and Feng (1999) showed that bamboo mortality was negatively correlated with canopy density, but studies by Uhl et al. (1988) indicated that gap sizes had no effect on mortality of bamboos. Ramet mortality of *F. nitida* in the FU was lower than that in the other conditions in our studies. The number of young ramets, number of simple bundle and biomass per ramet of *F. nitida* was lower in the FU, so their weakly intraspecific competition was helpful to survive for young ramets. By contrasting, in the LG, the number of young ramets and number of simple bundle of *F. nitida* was larger, which induced high mortality of young ramets by strong intraspecific competition. There were differences in ages of ramets, which meant the mean lifetime of *F. nitida* populations were the same in all conditions, and indicated that populations effectively adapt to different canopy conditions by morphological changes and biomass allocation of ramets. All the results indicated that it was not ramet age, but the morphological changes and biomass distribution that exhibited the response of the ramet population of *F. nitida* to changed canopy conditions.

In the subalpine forest, the light conditions were weaker in the understory and the growth of *F. nitida* ramet populations was poorer with the increase in the canopy density. Tree seedlings need more light than substrate (Qin et al., 1993), so the enhancement of light and photosynthetic active radiation (PAR) in the gap was in favor of the establishment of tree seedlings (Denslow et al., 1990, 1998). At the same time, with the decrease of canopy density, the flourishing shrub plants captured the light and nutrients crucial to the tree seedlings (Denslow et al., 1998; van der Meer et al., 1998). It could be considered that the environmental condition of the LG within plentiful bamboo growth in it was similar with that of the small gap and the FU (Tabarelli and Mantovani, 2000), so it will also influence the growth of tree seedlings. Moreover, it is hard for tree seedlings to establish and expand in the soil, especially about 40 cm under the ground surface, because the dwarf bamboo's rhizomes were more anfractuous with the decrease of canopy cover (Qin et al., 1993). During the field study, we found that in the gaps the bamboo grows better, and the number of *Abies faxoniana* was much fewer than that in

gaps that have same condition but little *F. nitida*. In addition, the distribution pattern of *F. nitida* population will be different under different canopy conditions, and it may be the critical factor that influences the growth and establishment of tree seedlings. The relationships between the distribution pattern of *F. nitida* and regeneration of the forest gap need further study.

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