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Effects of forest canopy gap on biomass of *Abies faxoniana* seedlings and its allocation in subalpine coniferous forests of western Sichuan

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Abstract Using a strip transect sampling method, the density, height (≤ 100 cm), basal diameter and components of biomass of *Abies faxoniana* seedlings, living in a forest gap (FG) and under the forest canopy (FC) of subalpine natural coniferous forests in western Sichuan, were investigated and the relationships among different components of biomass analyzed. The results indicated that the density and average height (H) of *A. faxoniana* seedlings were significantly different in the FG and under the FC, with the values being 12903 and 2017 per hm^2 , and 26.6 and 24.3 cm. No significant differences were found in the average basal diameter (D) and biomass. The biomass allocation in seedling components was significantly affected by forest gap. In the FG, the biomass ratio of branch to stem reached a maximum of 1.54 at age 12 and then declined and fluctuated around 0.69. Under the FC, the biomass ratio of branch to stem increased with seedling growth and exceeded 1.0 at about age 15. The total biomass and the biomass of leaves, stems, shoots and roots grown in the FG and under the FC were significantly correlated with D^2H . There were significant and positive correlations among the biomass of different components.

Keywords *abies faxoniana*, seedling, biomass, allocation pattern, subalpine, western Sichuan

1 Introduction

In 1947, Watt (1947) introduced the idea of canopy gap. During the 1980's, much attention has been paid to canopy gaps and this has become a major topic in forestry and ecology. The dynamics of canopy gaps form the mosaic of forest regeneration and the natural regeneration of forests is the process of formation, development and maturity of canopy gaps (Zhang et al., 1999). Therefore, the effect of canopy gaps on the generation of seedlings and saplings should be well understood and is important for the restoration and rebuilding of degraded ecosystems, for carrying out programs of natural forest conservation and for the scientific management of forest ecosystems. Currently, most studies of canopy gaps fastened on their characteristics (Shen et al., 2001), models (Sang and Li, 1998), microenvironments (Wang and Xu, 1995; Zhang et al., 2001), biodiversity (Wang et al., 2001) and other aspects. There are few reports related to the effect of canopy gaps on the growth of seedlings and saplings. Coniferous forests of the subalpine zone in western Sichuan, the second forest region of China, are one of the major regions of natural forest conservation program. The region is extolled as containing half of the water resources of China, as a major green ecological defense system and as a gene bank. These forests have been dominated by fir and spruce and the natural generations of these species have been hardly found under the densely closed canopy (less than 1000 trees per hm^2) and the generation in canopy gaps and forest edges is the major way for the generation of seedlings and saplings (more than 10000 trees per hm^2) (Yang, 1990; Yang et al., 1992). Following the practice of natural forest conservation, the following aspects, natural generation of forest, growth and development of naturally generated seedlings and

Translated from *Chinese Journal of Applied Ecology*, 2007, 18(4): 721–727 [译自: 应用生态学报]

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saplings and the regulation of these processes, have become urgent topics related to regional vegetation restoration and re-establishment and the management of forest ecosystems. Therefore, we have surveyed the development of seedlings in canopy gaps and under the forest in a typical subalpine forest zone of western Sichuan, southwestern China and measured their biomass. Our objectives were to understand the differences of seedling growth under various microenvironments and their adaptive mechanism by analyzing the biomass of the seedlings, their allocation and other factors. We trust our study will provide some positive evidence for understanding the development of fir and spruce seedlings, for the restoration and re-establishment of the sub-alpine, coniferous forests in western Sichuan and assist research in forest dynamics and the management of forests.

2 Study site and methods

2.1 General situation

Our experimental field was located in the Wanglang National Nature Reserve, a state-level nature protection area, belonging to the Pingwu County, Sichuan Province. The total area is 323 km² and characterized by Danba-Songpan semi-humid climate. It forms clear dry and wet seasons because of the effect of monsoons. The dry season, lasting from November to April, experiences intense sunshine, little rain and is cold and dry. The wet season, from May to October, is warm and wet, has much rain and fog but little sunshine. The average annual temperature is 2.9°C, 12.7°C in July and -6.1°C in January. The highest ever recorded temperature is 26.2°C and the lowest -17.8°C and the average annual accumulated temperature ($\geq 10^\circ\text{C}$) is 1056.5°C. Average annual precipitation is 859.9 mm, concentrated mainly from May to July.

The elevation of the region is between 2400 and 4980 m, with an obvious height discrepancy of 2500 m and an average elevation above 3200 m. At the lower elevations (2300–2850 m), the soil is a mountainous, regional brown earth, from 2600–3500 m the soil is a mountainous, regional dark brown earth, a subalpine meadow soil at 2300–3500 m on sunny slopes, a mountain meadow soil from 3500–4000 m and a mountain flowstone beach desert soil at elevations over 4000 m. The vertical distribution of vegetation consists of conifer-broadleaf mixed forest at 2300–2600 m, *Sabina saltuaria*–*Picea purpurea* mixed forests and *Abies faxoniana* forests at 2600–3500 m, subalpine brush meadows at 3500–4400 m, mountain flowstone beach plants at 4400–4900 m and an alpine desert belt over 4900 m elevation (Xian et al., 2004a, 2004b).

Abies faxoniana–*Fargesia denudata*–*Hylocomium splendens* communities are mainly found on river terraces at

elevations between 2800–3100 m. The average age of the forest is about 180 years. The average height and diameter at breast height are 38 and 45 cm, respectively. The dominant tree species is *Abies faxoniana* and the subdominant tree layer consists largely of *Sabina saltuaria* with some *Acer* spp. The canopy closure is between 0.4–0.6. The shrub floor mainly includes *Fargesia denudata* Yi, *Lonicera* spp., *Abies faxoniana* and young maple seedlings. The average height of the shrub species is 1.4 m and the coverage is 40%. The grass floor, with an average height of 30 cm and coverage of 30%, is made up of *Cardamine tangutorum*, *Smilacina japonica* and ferns. The moss layer is 8 cm thick with more than 90% coverage, consisting of *Abietinella abietina* and *Hylocomium splendens*.

2.2 Research methods

2.2.1 Data collection

We randomly set three transects perpendicular to the contour line, 300 m long and 2 m wide each, with spacing over 20 m. For the sake of convenience, we assume the height of all *A. faxoniana* seedlings (seedling for short hereinafter) as less than 100 cm. We carefully dug up the seedlings grown under the forest canopy (FC) and in the forest gaps (FG), cleaned the roots with clean water and dried them. We measured the basal diameter (D), height (H), the weight of fresh roots, of fresh leaves, of fresh stems (trunk and branches) and of each seedling and then sampled from different organs of sampled seedlings. We placed the seedlings in a ventilated drying oven at 80°C to obtain their final equilibrium weight and finally we calculated the biomass of each organ.

2.2.2 Data processing

In our study, we ascertained the age of the seedling by counting the annual rings at the basal diameter and branch rings. We used the following criteria to distinguish seedling, in years, by age (A) classes: class I, $A \leq 3$ years; class II, $3 < A \leq 6$ years; class III, $6 < A \leq 9$ years; class IV, $9 < A \leq 12$ years; class V, $12 < A \leq 15$ years; class VI, $A > 15$ years.

The transect was only 2 m wide, so we used the area of transect within the forest gap (FG) as our gap area. We used the following definitions in our study: the density of seedlings in the FG = the number of seedlings in the FG/area of the FG and seedling density under the forest canopy (FC) = the number of seedlings under the FC/area under the FC. The total seedling biomass = leaf biomass + root biomass + stem biomass; stem biomass = trunk biomass + branch biomass; ground biomass = leaf biomass + stem biomass. Leaf biomass ratio = leaf biomass/total seedling biomass; the biomass ratio of root to stem = dry root substance/stem biomass; branch biomass ratio =

branch biomass/total seedling biomass. The ratio of height to basal diameter = H/D ; the biomass ratio of leaf to root = leaf biomass/root biomass, and the biomass ratio of canopy to root = ground biomass/root biomass.

3 Results and analysis

3.1 Average height, basal diameter and density of *A. faxoniana*

There was a total of 768 seedlings (288 under the FC, 480 in the FG) in the three sample transects. Of the entire sample transect area, that of the FG was 372 m², accounting for 21% and the area under the FC was 1428 m², accounting for 79%. Seedling density of the FG was 12903 per hm², with an average basal diameter of 4.97 mm and the average height of the seedlings was 26.6 cm. Seedling density under the FC was 2017 per hm², with the average basal diameter at 5.13 mm and the average height at 24.3 cm. The density and average height of seedlings in the FG were higher than under the FC (Table 1). The opposite was true for basal diameter. The differences in basal diameter for each age class in the FG and under the FC were statistically not significant ($F = 1.148, p > 0.05$), but the differences in seedling height were significant ($F = 20.618, p < 0.05$).

3.2 Biomass of *A. faxoniana* seedlings

3.2.1 Absolute value of component biomass

The differences of seedling biomass at each age class in the FG and under the FC were not significant ($F_1 = 2.034,$

$F_{II} = 1.889, F_{III} = 0.327, F_{IV} = 2.729, F_V = 0.282, F_{VI} = 0.997, p > 0.05$). The differences in root biomass at each age class in the FG and under the FC were also not significant ($F_1 = 1.316, F_{II} = 0.014, F_{III} = 2.907, F_{IV} = 2.556, F_V = 0.861, F_{VI} = 0.764, p > 0.05$). These results show that the FG and FC had no remarkable effects on the accumulation of seedling biomass and underground root portion (Table 2).

The leaf biomass at each age class in the FG was higher than under the FC and shows highly significant differences in age classes II, III and IV ($F_{II} = 8.525, F_{III} = 7.619, F_{IV} = 11.023, p < 0.01$), but the differences in the I, V and VI age classes were not significant ($F_1 = 3.410, F_V = 0.485, F_{VI} = 0.719, p > 0.05$). The stem biomass at each age class in the FG was also higher than under the FC. Highly significant differences existed in age classes III, IV and V ($F_{III} = 8.585, F_{IV} = 6.594, F_V = 6.059, p < 0.01$), but the differences in age classes I, II and VI were not significant ($F_1 = 1.037, F_{II} = 0.006, F_{VI} = 0.018, p > 0.05$). These results indicate that the amounts of biomass of leaves and stems at several age classes of *A. faxoniana* seedling in the FG were greater than those of seedlings grown under the FC.

3.2.2 Component biomass ratio

The leaf biomass of *A. faxoniana* seedlings in the FG was higher than under the FC (Table 3). There were very significant differences in each age class except for I and VI ($F_{II} = 37.555, F_{III} = 77.811, F_{IV} = 12.118, F_V = 23.191, p < 0.01$). The difference of stem biomass ratio was entirely consistent with that of its leaf biomass ratio, but the stem biomass ratio under the FC was higher than the ratio in the FG (except for age class IV). The biomass

Table 1 Height of *A. faxoniana* seedlings for different age classes in forest gap and under canopy

age class	forest gap				under canopy			
	mean \pm S.D./cm	max./cm	min./cm	number of trees	mean \pm S.D./cm	max./cm	min./cm	number of trees
I	12.1 \pm 2.94	19.2	7.2	22	10.0 \pm 1.5	12.4	7.4	17
II	17.6 \pm 4.8	30.3	8.5	158	15.2 \pm 4.6	39.2	7.6	73
III	25.7 \pm 6.0	47.5	11.9	164	21.3 \pm 5.4	37.4	10.5	90
IV	33.2 \pm 5.2	44.5	22.2	91	29.2 \pm 6.3	44.5	17.3	64
V	41.3 \pm 8.2	56.4	22.4	37	37.0 \pm 7.4	56.4	24.2	33
VI	59.1 \pm 10.4	82.5	34.5	8	43.2 \pm 7.5	54.5	29.2	11

Table 2 Average component biomass of *A. faxoniana* seedlings for different age classes in FG and under forest canopy (mean \pm S.D.)

age class	leaf biomass/g		stem biomass/g		above-ground biomass/g		root biomass/g		total biomass/g	
	A	B	A	B	A	B	A	B	A	B
I	0.33 \pm 0.18	0.23 \pm 0.11	0.18 \pm 0.01	0.07 \pm 0.04	0.51 \pm 0.27	0.30 \pm 0.15	0.11 \pm 0.00	0.20 \pm 0.01	0.62 \pm 0.28	0.50 \pm 0.22
II	0.95 \pm 0.49	0.76 \pm 0.46	0.70 \pm 0.40	0.35 \pm 0.20	1.65 \pm 0.87	1.10 \pm 0.62	0.41 \pm 0.25	0.42 \pm 0.211	2.07 \pm 1.05	1.52 \pm 0.76
III	2.71 \pm 1.08	2.32 \pm 0.98	2.24 \pm 0.98	1.34 \pm 0.65	4.95 \pm 1.99	3.65 \pm 1.49	1.24 \pm 0.62	1.39 \pm 0.67	6.19 \pm 2.46	5.04 \pm 2.43
IV	5.92 \pm 1.61	4.92 \pm 1.99	8.41 \pm 2.19	3.79 \pm 2.31	14.33 \pm 3.75	8.72 \pm 3.63	2.97 \pm 1.23	3.30 \pm 1.19	17.30 \pm 4.64	12.2 \pm 5.13
V	10.87 \pm 4.12	10.22 \pm 4.81	10.37 \pm 3.96	6.60 \pm 2.83	21.25 \pm 7.73	16.83 \pm 7.29	5.52 \pm 2.18	6.25 \pm 2.36	26.77 \pm 9.32	23.08 \pm 8.89
VI	17.71 \pm 5.51	15.41 \pm 5.04	21.19 \pm 7.27	10.39 \pm 3.81	38.89 \pm 11.99	25.80 \pm 8.69	9.57 \pm 1.62	9.99 \pm 3.08	48.47 \pm 13.16	34.89 \pm 10.87

A: in the forest gap; B: under forest canopy. The same identification applies to following tables.

Table 3 Leaf biomass ratio, stem biomass ratio, biomass ratio of root to stem, ratio of height to basal diameter of *A. faxoniana* seedlings (mean ± S.D.)

age class	leaf biomass ratio		stem biomass ratio		biomass ratio of root to stem		ratio of height to basal diameter	
	A	B	A	B	A	B	A	B
I	0.50 ± 0.02	0.46 ± 0.01	0.29 ± 0.01	0.29 ± 0.02	0.72 ± 0.09	0.81 ± 0.02	6.89 ± 0.38	5.95 ± 0.39
II	0.46 ± 0.00	0.40 ± 0.01	0.33 ± 0.05	0.37 ± 0.01	0.65 ± 0.03	0.71 ± 0.05	5.66 ± 0.10	4.90 ± 0.17
III	0.44 ± 0.00	0.36 ± 0.01	0.36 ± 0.00	0.41 ± 0.01	0.58 ± 0.02	0.58 ± 0.03	5.19 ± 0.08	4.36 ± 0.12
IV	0.34 ± 0.00	0.32 ± 0.01	0.49 ± 0.00	0.46 ± 0.01	0.35 ± 0.01	0.51 ± 0.03	4.87 ± 0.08	4.23 ± 0.12
V	0.41 ± 0.00	0.33 ± 0.01	0.38 ± 0.01	0.43 ± 0.01	0.57 ± 0.03	0.61 ± 0.09	4.62 ± 0.15	4.16 ± 0.13
VI	0.37 ± 0.02	0.33 ± 0.01	0.42 ± 0.02	0.43 ± 0.00	0.52 ± 0.07	0.58 ± 0.05	4.40 ± 0.61	3.88 ± 0.12

ratio of root to stem in each age class under the FC was higher than in the FG. The difference in the biomass ratio of root to stem in each age class was not significant ($F_I = 3.423$, $F_{II} = 1.327$, $F_{III} = 0.005$, $F_V = 0.250$, $F_{VI} = 0.257$, $p > 0.05$), except for age class IV for which the difference was highly significant ($F_{IV} = 30.295$, $p < 0.05$). The leaf biomass ratio in age class IV was the lowest in both the FG and under the FC, but the result was just the opposite in the stem biomass ratio. The reason may be that the average height of seedlings in age class IV was about 30 cm, which was the same height as that of the grass floor in the forest community, so there was intense competition for sunlight with the result that part of leaves dried up, but the branches remained.

Along with the seedling growth, the ratio of height to basal diameter decreased in the FG and under the FC, the ratio of height to basal diameter in the FG was larger than that under the FC. Their difference was significant ($F_I = 3.853$, $F_{II} = 17.094$, $F_{III} = 34.034$, $F_{IV} = 20.859$, $F_V = 5.107$, $F_{VI} = 16.478$, $p < 0.05$). We conclude that the conditions in the FG were good for height growth of *A. faxoniana* seedlings.

As shown in Table 4, the biomass ratio of leaf to root in the FG (2.48 ± 1.12 on average) was higher than for the seedlings of the same age classes grown under the FC (1.84 ± 0.89 on average). These differences are very significant ($F = 68.865$, $p < 0.01$). The average biomass ratio of canopy to root in the FG and under the FC, respectively, was 4.65 ± 1.91 and 2.88 ± 1.27 and their difference is also very significant ($F = 194.864$, $p < 0.01$).

From Table 4, we can see that the biomass ratio of branch to stem increased with the seedling growth and reached its maximum (1.54) in about 12 years, then

quickly decreased and maintained at around 0.69. In the entire growing period of seedlings grown under the FC, the ratio of branch to stem increased all the time. In the 15th year, it reached 1.10 ± 0.33 . The substance accumulated in branches exceeded that in stems, which indicates the growth of seedlings was predominated by the growth of lateral branches when approaching age class V (the 15th year). At the beginning of the growing period (age class IV, before the 14th year), the difference of substance accumulation in branches is not significant for seedlings in the FG and under the FC. After the 14th year, the above-ground substance accumulation changed markedly for seedlings in the FG and under the FC, the former mainly in stems and the latter largely in branches. This result shows that the environment of FG has an important effect to the growth of seedlings, especially in the later growing period. We can reach a similar conclusion though the analysis of the branch biomass ratio under different conditions.

3.3 The relationship of biomass among different organs

3.3.1 The relationship among biomass of each component

As shown in Figs. 1 and 2, for seedlings with the same above-ground biomass under the FC and in the FG, the former was higher than the latter in underground biomass. It indicates that more biomass was allocated in roots in the FG. The above-ground biomass, underground biomass, leaf biomass and stem biomass all had a significant linear relationship with the total biomass of seedlings grown in the FG and under the FC.

Table 4 Biomass ratio of leaf to root, biomass ratio of canopy to root, biomass ratio of branch to stem, branch biomass ratio of *A. faxoniana* seedlings (mean ± S.D.)

age class	biomass ratio of leaf to root		biomass ratio of canopy to root		biomass ratio of branch to stem		branch biomass ratio	
	A	B	A	B	A	B	A	B
I	3.61 ± 2.08	2.21 ± 0.93	2.56 ± 1.13	2.95 ± 1.32	0.13 ± 0.14	0.10 ± 0.58	0.03 ± 0.03	0.03 ± 0.04
II	2.66 ± 1.27	1.96 ± 0.91	4.58 ± 2.14	2.85 ± 1.21	0.30 ± 0.16	0.43 ± 0.21	0.08 ± 0.03	0.11 ± 0.05
III	2.42 ± 0.93	1.89 ± 0.98	4.40 ± 1.60	2.95 ± 1.36	0.43 ± 0.22	0.70 ± 0.29	0.11 ± 0.03	0.17 ± 0.06
IV	2.20 ± 0.72	1.65 ± 0.81	5.33 ± 1.74	2.91 ± 1.38	1.54 ± 0.32	0.85 ± 0.32	0.29 ± 0.02	0.22 ± 0.05
V	2.09 ± 0.65	1.77 ± 0.95	4.05 ± 1.14	2.91 ± 1.45	0.69 ± 0.24	1.10 ± 0.33	0.16 ± 0.04	0.22 ± 0.06
VI	1.85 ± 0.50	1.60 ± 0.44	4.03 ± 0.95	2.68 ± 0.75	0.68 ± 0.23	1.11 ± 0.38	0.17 ± 0.04	0.24 ± 0.05

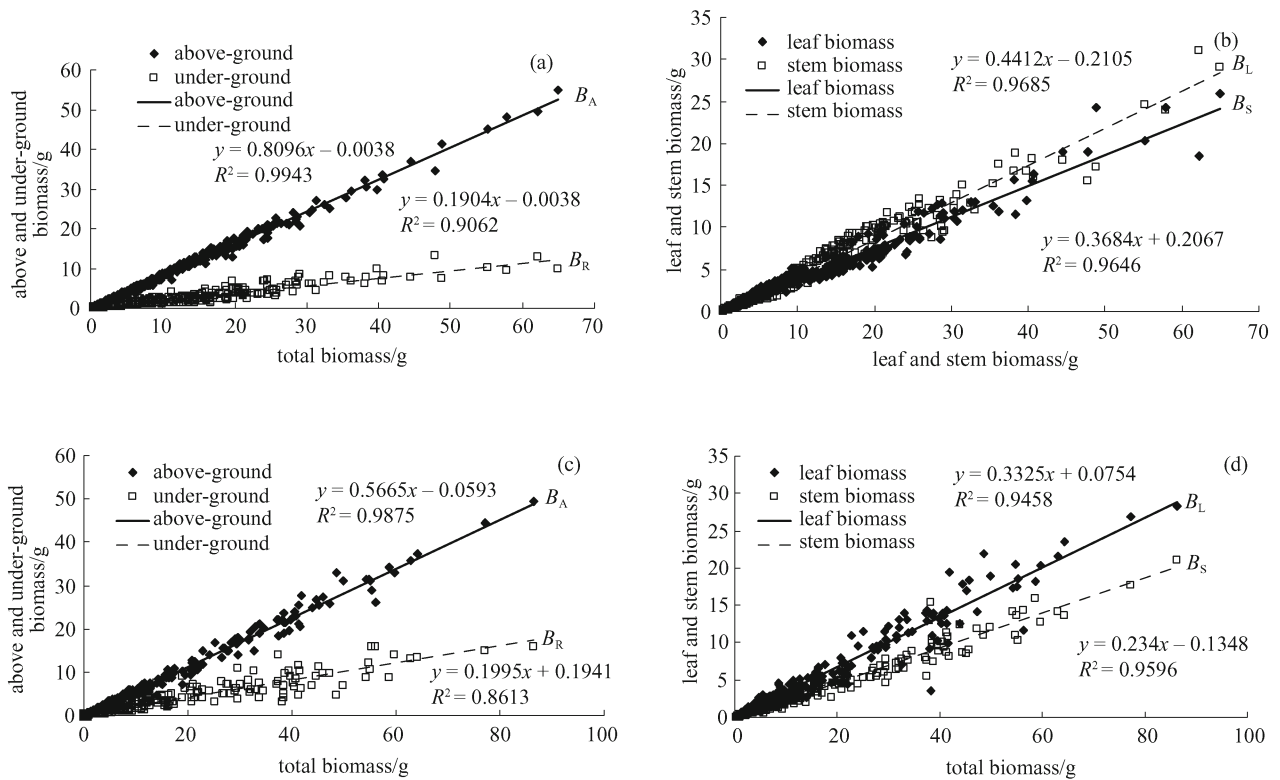


Fig. 1 Relationship of root, above-ground, leaf, stem and the total biomass of *A. faxoniana* seedlings (a), (b): in the forest gap; (c), (d): under forest canopy. B_A , B_R , B_L and B_S mean biomass of above-ground parts, roots, leaves and stems, respectively

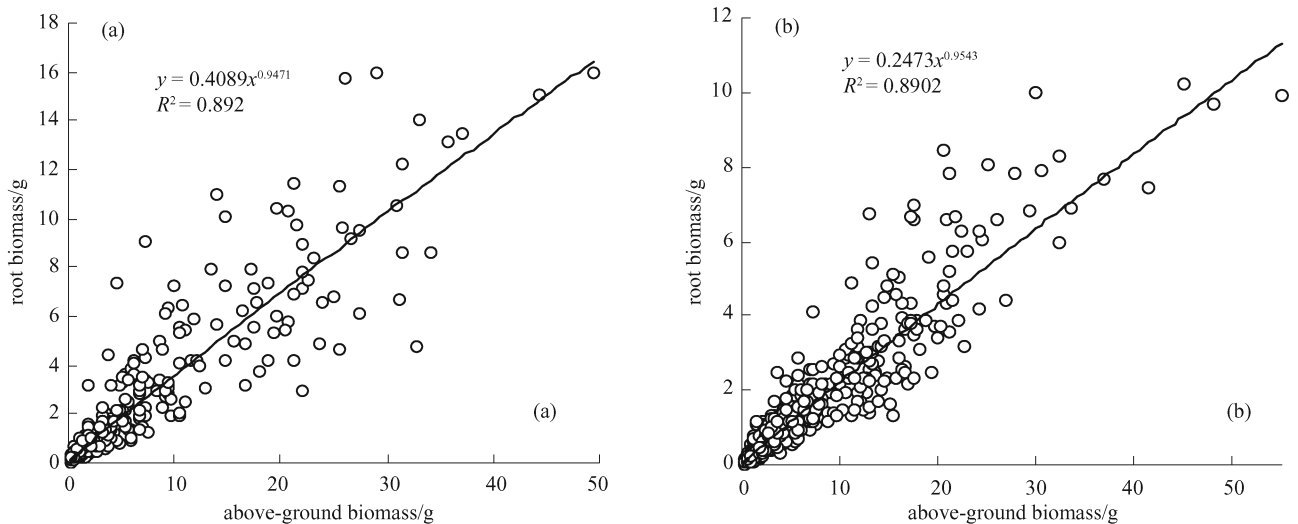


Fig. 2 Exponential regression between above- and under-ground biomass of seedlings (a) in the forest gap; (b) under forest canopy

3.3.2 The relationship between biomass of each component and basal diameter or height of seedlings

From Fig. 3, we can see that the biomass of single seedling (B_T) had a significant linear relationship with the square of basal diameter (D^2) and height (H). The biomass of leaf (B_L), stem (B_S), above-ground part (B_A) and root (B_R) were significantly linearly correlated with D^2H .

4 Discussion

4.1 Biomass of *A. faxoniana* seedlings

The findings of this study indicate that the average biomass, leaf biomass and stem biomass of a single seedling grown in the FG were all higher than that grown under the FC, but the opposite was true for the average root

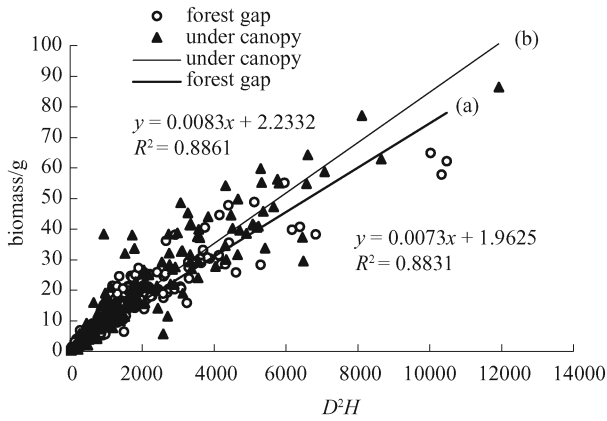


Fig. 3 Line regression between total biomass of *A. faxoniana* seedling and D^2H
(a): in the forest gap; (b): under forest canopy

biomass. Previous studies indicated that the solar radiation in the FG and under the FC respectively accounted for $(31.84 \pm 8.20)\%$ and $(17.63 \pm 5.49)\%$ of that in the open space outside the forest, and difference of the radiation intensity in the FG and under the FC was highly significant (Wang, 2004). The biomass of seedlings grown in the FG was higher than that under the FC, suggesting that the accumulation of dry substance in *A. faxoniana* seedlings increased with the enhancement of light. The difference of biomass of seedlings of each age class was not marked, indicating that, besides sunlight, there were also some other affecting factors. Presently, there have already been some studies pointing out that the factors such as the effectiveness of soil nutrients and shrub layer had crucial effects on seedling growth. Bungard et al. (2000) suggested that the effective soil nutrients (especially effective nitrogen) were one of factors limiting seedling growth. Beckage et al. (2000) and Tabarelli and Mantovani (2000) believed that the shrub layer had remarkable inhibitory effects on the growth of arbor seedlings. Taylor and Qin (1988) also pointed out that the density of *Fargesia spathacea* Franch., a dominant species in the shrub layer in *A. faxoniana* forest, affected the regeneration of arbor species and seedling growth. Howe (1990) thought that the herb species and canopy closure had significant effects on the survival and growth of seedlings. Therefore, an in-depth study of shrub layer, soil nutrients, water, soil temperature and CO_2 concentration is necessary in order to better reveal the effects of forest gap of subalpine natural coniferous forests in western Sichuan on the growth and biomass distribution of *A. faxoniana* seedlings.

4.2 The biomass ratio of leaf to root and canopy to root of *A. faxoniana* seedlings

The present study found that the difference of average biomass ratio of leaf to root in the FG and under the FC was very significant at 2.48 ± 1.12 and 1.84 ± 0.89 , respectively. The average biomass ratio of canopy to root

under the two conditions had also high difference ($p < 0.01$) at 4.65 ± 1.91 and 2.88 ± 1.27 , respectively.

Temperature and humidity were two important factors affecting the biomass ratio of canopy to root. Lyr and Garbe (1995) found that soil temperature affected the ratio of root to stem of *Fagus sylvatica* seedlings. Generally speaking, air temperature and vapor pressure deficit (VPD) in the FG is higher than that under the FC, which in result leads to a higher transpiration rate in the FG, and gives rise to water stress. Water stress will restrain photosynthesis and limit the accumulation of seedling biomass to adapt to the adverse environment. Usually, in response to water stress, plants will redistribute its biomass, assigning more biomass to the roots to enhance the water-absorption ability of the roots. Therefore, under water stress, plants possess a high biomass ratio of root to stem. After the cessation of water stress, the biomass ratio of root to stem of *Fagus sylvatica* declined with the increase of sunlight intensity and the carbohydrate amounts assigned to the roots will be reduced if no competition for soil nutrients occurs (Lyr and Garbe, 1995). The interaction between sunlight and soil also significantly affected the biomass distribution situation (King, 1994; Minotta and Pinzauti, 1996; Guo and Werger, 1999). Some other studies found that the sunlight under the FC, rather than soil, limited the growth and development of seedlings (Norgren, 1996; Gardiner and Hodges, 1998). In the present study, the biomass ratio of root to stem in the FG was lower than that under the FC because of the strong water-holding capacity of forest community in the FG (there was 10 cm deep moss floor under the virgin forest) and high air humidity. Under such conditions, plants can usually be free of water stress in their growing period, so the biomass ratio of root to stem of most seedlings of the same age class had no marked difference. The biomass ratio of root to stem of seedlings of age class IV had marked difference between the FC and FG, and it might be explained by that the grass floor in the FG developed well and had almost the same height with seedlings of age class IV.

4.3 Application of biomass distribution pattern of *A. faxoniana* seedlings

The growth of *A. faxoniana* seedlings in the FG and under the FC was similar before 14 years age. After the 15th year, the seedling biomass under the FC was mostly accumulated in branches, but evenly distributed for seedlings in the FG. Field investigation also indicated that, under the FC, the biomass increment of the lateral branches of *A. faxoniana* seedlings of 15 years age was obvious and it was even more obvious for those of 17–20 years age with a slow growth of stem and death of apical buds. Such phenomenon could not be found in the FG. Our field observations indicated that shade-tolerant tree species could grow under the FC or in the shady FG, but there must be the forest gap that can provide sufficient sunshine and

space for seedlings to develop and reach the main storey. Our results were consistent with the findings of other scientists (Yang et al., 1992; Wang and Xu, 1995). The time that the lateral branches of seedlings start a quick growth, from 15 years age in the present study, was later than that in others studies, which might be because of the difference of plant species of interest.

Occurrence of forest gaps could give rise to changes in such factors as micro-topography, light environment, air temperature and humidity and soil nutrients (Zang et al., 1999), which caused large heterogeneity in the forest environment and provided more opportunities and space for the germination and growth of seedlings. This enables the normal regeneration of the forest and an accommodation of more species. Occurrence of the forest gaps is significant for the germination and growth of seedlings. Szwagrzyk et al. (2001) indicated that normal growth of seedlings of shade-tolerant tree species need occurrence of the forest gaps, too. Diaci (2002) thought that successful forest regeneration could be accomplished by controlling geometric features like size, shape and direction of forest gaps. So, we can increase small-scale interference to promote smooth forest succession and sustain higher biodiversity in the forest ecosystem management. In highly closed climax communities, we can obtain sufficient illumination and space for the growth of shade-tolerant tree species and create conditions artificially for the regeneration of heliphilous tree species (for example, in virgin forests, heliphilous tree species like *Betula* spp. can only be found in the FG). In the degraded forest ecosystem, we can fell broad-leaved trees to promote the growth of coniferous species. In communities which are in their early successional stages and the community or dominated by heliphilous tree species, shade-tolerant tree species can regenerate naturally with the aid of shade. Or, we can artificially make forest gaps to help the trees grow quickly. However, too frequent occurrence of forest gaps and interference would make forests degenerate quickly (Vogt et al., 2002). So in the forest ecosystem management, we can properly increase small-scale interference but should prevent large-scale interference and frequent occurrence of forest gaps in order to sustain the stability and biodiversity of the forest ecosystem (Zhong, 1997).

Acknowledgements This study was funded by the National Natural Science Foundation of China (Grant Nos. 90511008 and 902020100), the Corporation Foundation of China and Finland (No. 30211130504) and the Technology and Science Innovation Foundation of Sichuan Province, China (No. 05SG023-009).

References

Beckage B, Clark J S, Clinton B D, Haines B L (2000). A long-term study of tree seedling recruitment in southern application forests: The effects of canopy gaps and shrub understories. *Can J For Res*, 30(10): 1617-1631

- Bungard R A, Scholes J D, Press M C (2000). The influence of nitrogen on rain forest dipterocarp seedling exposed to a large increase in irradiance. *Plant Cell Environ*, 23(11): 1183-1194
- Diaci J (2002). Regeneration dynamics in a Norway spruce plantation on a silver fir-beech forest site in the Slovenian. *For Ecol Manage*, 161(1-3): 27-38
- Gardiner E S, Hodges J D (1998). Growth and biomass distribution of cherrybark oak (*Quercus pagoda* Raf.) seedlings as influenced by light availability. *For Ecol Manage*, 108(1-2): 127-134
- Guo K, Werger M J A (1999). Different responses to shade of evergreen and deciduous oak seedlings and the effect of acorn size. *Acta Oecol*, 20(6): 579-586
- Howe H F (1990). Survival and growth of juvenile *Virola surinamensis* in Panama: Effects of herbivory and canopy closure. *J Trop Ecol*, 6(3): 259-280
- King D A (1994). Influence of light level on the growth and morphology of saplings in a Panamanian forest. *Amer J Bot*, 81 (8): 948-957
- Lyr H, Garbe V (1995). Influence of root temperature on growth of *Pinus sylvestris*, *Fagus sylvatica*, *Tilia cordata* and *Quercus robur*. *Trees*, 9(4): 220-223
- Minotta G, Pinzauti S (1996). Effects of light and soil fertility on growth, leaf chlorophyll content and nutrient use efficiency of beech (*Fagus sylvatica* L.) seedlings. *For Ecol Manage*, 86(1-3): 61-71
- Norgren O (1996). Growth analysis of Scots pine and lodgepole pine seedlings. *For Ecol Manage*, 86(1-3): 15-26
- Sang W G, Li J W (1998). Dynamics modeling of Korean pine forest in southern lesser Xingan mountains of China. *Acta Ecol Sin*, 18(1): 38-47 (in Chinese)
- Shen Z H, Li D X, Wang G F (2001). Studies on the gap disturbance of the mountain mixed forests of evergreen and deciduous broad-leaved species at MT. Dalaoling in the three Gorges I. The essential characteristics of the gaps. *Acta Phytoecol Sin*, 25 (3): 276-282 (in Chinese)
- Szwagrzyk J, Szewczyk J, Bodziarczyk J (2001). Dynamics of seedling banks in beech forest: results of a 10-year study on germination, growth and survival. *For Ecol Manage*, 141(3): 237-250
- Tabarelli M, Mantovani W (2000). Gap-phase regeneration in a tropical mountain forest: the effects of gap structure and bamboo species. *Plant Ecol*, 148(2): 149-155
- Taylor A H, Qin Z S (1988). Regeneration patterns in old-growth *Abies-Betula* forests in the Wolong Natural Reserve, Sichuan China. *J Ecol*, 76(4): 1204-1218
- Vogt K, Gordon J, Wargo J (2002). *Ecosystem: the Science of Balance and Management* (in Chinese, trans. Ouyang H). Beijing: Science Press (in Chinese)
- Wang J X, Xu J D (1995). *Logging-clearing Ecology, Forest Management and Regeneration Technology of Alpine Forest Zone in the Upper Reach of the Yangtze River*. Beijing: China Forestry Publishing House (in Chinese)
- Wang K Y (2004). *Processes of Subalpine Forest Ecosystem in the West of Sichuan*. Chengdu: Sichuan Science and Technology Publishing House (in Chinese)
- Wang Z P, Li X G, Shi S Y, Qi D H, He Z M, Xu W W, Deng X B (2001). Gap phase tree replacement in a conifer-broadleaved mixed forest in Jinyun mountain, Chongqing. *Acta Phytoecol Sin*, 25(4): 399-404 (in Chinese)
- Watt A S (1947). Pattern and process in the community. *J Ecol*, 35(1-2): 1-22
- Xian J R, Hu T X, Wang K Y, Zhang Y B, Zhu X M, Xu J W (2004). Studies on the characteristics of gap border trees in the subalpine coniferous forest in western Sichuan. *For Res*, 17(5): 36-42 (in Chinese)
- Xian J R, Hu T X, Zhang Y B (2004). Characteristics of gap in subalpine coniferous forest in western Sichuan. *Chin J Ecol*, 23(3): 6-12 (in Chinese)

- Yang Y P (1990). Review on forest defense function in western Sichuan Province. In: Li C B, ed. Ecological Study on Sichuan Forest. Chengdu: Sichuan Publishing House of Science and Technology. 49–54 (in Chinese)
- Yang Y P, Li C B, Guan Z T (1992). Forests in Sichuan. Beijing: China Forestry Publishing House (in Chinese)
- Zang R G, Liu J Y, Dong D F (1999). Gap Dynamics and Forest Biodiversity. Beijing: China Forestry Publishing House
- Zhang Y P, Wang J X, Ma Y X (2001). Characteristics analysis on different thermal active surface in canopy gap of tropical secondary forest. *Chin J App Ecol*, 12(2): 179–184 (in Chinese)
- Zhong Z C (1997). Ecosystem and environmental protection. In: Zhong Z C, ed. *Advance in Plant Ecological Research*. Chongqing: Publishing House of Southwest China Teachers University, 653–665 (in Chinese)