Original Article

Influence of topography, soil properties and plant community on the biomass of *Abies georgei* var. *smithii* seedlings in Southeast Tibet

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Abstract: Biomass of seedlings at different developing stages of growth is important information for studying the response of species to site conditions. The objectives of this study was to explore the distribution characteristics of AGB (above-ground biomass) and BGB (below-ground biomass) of *Abies georgei* var. *smithii* seedlings of different ages, and investigate the effects of topography (slope aspect, altitude), plant community characteristics (crown density, species diversity, etc.), and soil properties (soil physical and chemical properties) on the biomass and its allocation. Seedlings in five age classes (1–2, 3–4, 5–6, 7–8, and 9–10 years old) were collected by full excavation from 6 elevations (3800 m, 3900 m, 4000 m, 4100 m, 4200 m, 4300 m) on the north and south slopes of Sejila Mountain in Tibet. 15 seedlings of each age class were investigated at one altitude. The individual effects of seedling age (SA) and the interaction effects of SA, slope aspect (SL),

and elevation (EG), namely, SL×EG, SL×SA, EG×SA, and SL×EG×SA, had significant effects on the AGB of the seedlings ($p<0.05$), whereas BGB was only significantly affected by SA ($p<0.001$). The AGB and BGB of the seedlings showed a binomial growth trend with the increase in seedling age, and had an allometric relationship at different elevations, α (allometric exponential) varied from 0.913 to 1.046 in the northern slope, and from 1.004 to 1.268 in the southern slope. The biomass of seedlings on the northern slope was remarkably affected by stand factors, with a contribution rate of 47.8%, whereas that on the southern slope was considerably affected by soil factors with a contribution rate of 53.2%. The results showed that age was the most important factor affecting seedling biomass. The allometric pattern of seedling biomass was relatively stable, but in a high-altitude habitat, *A. georgei* var. *smithii* seedlings increased the input of BGB. Understanding seedling biomass allocation and its influencing factors is useful for evaluating plants' ability to acquire resources and survival strategies for adaptation to the environment in Tibet Plateau.

1 Introduction

Seedling stage is a critical period in the life cycle of tree species (Comita et al. 2010), during which biomass allocation pattern determines the photosynthetic efficiency and planting cost of seedlings (Ding et al. 2016). According to optimal allocation theory, plants will preferentially allocate more biomass to tissues with limited resources (Gargaglione et al. 2010), which means that plants will allocate more biomass to leaves and branches if light becomes more limited, and plants will allocate more biomass to roots if water or nutrients become limited (Mokany et al. 2006; Ryser and Eek 2000). Biomass allocation patterns may affect the carbon storage of developing seedlings through the transformation of photosynthetic "source" to respiratory "sink" in plants (Modrzyński et al. 2015). Although biomass allocation has been studied deeply in tree species (Parresol 2001; Bi et al. 2004; Peichl and Arain 2007; Gargaglione et al. 2010), the patterns of plant biomass allocation under competitive stress are not consistent among different tree species(Xue et al. 2010; Konôpka et al. 2020; Konôpka et al. 2021; Wertz et al. 2020).The survival mechanism of different plant seedlings to adapt to high-altitude resource-deficient habitat through biomass allocation is still not full understood.

Different biomass components have different functions, especially in photosynthetic uptake of carbon. Peng et al. (2019) reported that the degradation of alpine grassland on the Qinghai-Tibet Plateau resulted in the increase of belowground biomass and the decrease of aboveground biomass. Biomass allocation patterns not only play an important role in resource acquisition and survival competition (Hermans et al. 2006; Poorter et al. 2012), but also been used to assess plant responses to environmental changes (Peng et al. 2019; Sun et al. 2017). Nie et al. (2019) found that soil properties, topography, and landform affected the understory biomass of subtropical hilly pine forest. Zhang et al. (2016) found stand characteristics and environmental factors significantly affected forest biomass and root cap allocation in Southwest China. Xiang et al. (2020)

reported the biomass allocation and allometric growth equation of *Cunninghamia lanceolata* were affected by stand age. Stand age affects tree size, shape, biomass allocation, and consequently allometric relationships (Peichl and Arain 2007). As stands develop, there are considerable changes in micro-site conditions (e.g. such as light and soil nutrients) and the interactions among individual trees to acquire available resources. Accordingly, tree shape (taper), crown structure and root systems vary with stand age so that allometric relationships between tree biomass components and dimensional variables differ greatly (Peichl and Arain 2007; Fatemi et al. 2011). Therefore, when developing allometric equations for tree biomass components, the effects of stand age should be taken into account to minimize the bias.

Abies georgei var. *smithii* is the dominant species of the natural dark coniferous forest in Sejila Mountain in Southeast Tibet and has important ecological functions, such as water and soil conservation, and serves as an ecological security barrier in the Qinghai–Tibet Plateau. However, natural regeneration is difficult because of the degradation of forest ecological environment. The natural distribution area of *A. georgei* var. *smithii* shrunk, and the population number decreased (Wang et al. 2014; Liang et al. 2010). The seedling stage is crucial for forest's regeneration, survival and performance at this stage will affect the composition, structure, and function of forest ecosystems in the future (Modrzyński et al. 2015). Biomass allocation patterns reflect the different ecological strategies of plants (Weiner 2004), which reflect the investment of photosynthates in different parts of plants to adapt to environmental conditions (Niklas 2006; Poorter and Sack 2012). There are few comprehensive studies on the effects of environmental factors (topographic factors, stand characteristics, soil properties, etc.) to the biomass allocation of *A. georgei* var. *smithii* seedlings in Southeast Tibet. Therefore, we studied biomass and its allocation of *A. georgei* var. *smithii* seedlings typically to answer three main questions: (i) how is the distribution characteristics of AGB (above-ground biomass) and BGB (below-ground biomass) of *A. georgei* var. *smithii* seedlings in different slopes, elevations, and seedling ages? (ii) Does the biomass of *A. georgei* var. *smithii* seedlings followed an allometric pattern in alpine ecosystem? (iii) how does topographic, stand characteristics, and soil properties affect biomass of *A . georgei* var. *smithii* seedlings in

subalpine high-altitude habitats?

2   Materials and Methods

2.1 Study area

The study site is located in Sejila Mountain (93°12′–95°35′ E, 29°10′–30°15′ N) in Nyingchi City, Tibet Autonomous Region, China (Fig. 1). Sejila Mountain is close to the branch of the Yarlung Zangbo River (Niyang River basin) with an altitude of 2100–5300 m, and is a part of the Nyenqing Tanggula Mountains (Zhou et al. 2015). This region is characterized by typical warm temperate and temperate mountain climates with distinct dry and wet seasons. The annual temperature amplitude ranges from –13.98 ℃ to 9.23 ℃, and the annual average temperature is –0.73 ℃ (Wang et al. 2019). Most of the rainfall occurs from June to September, and the precipitation can exceed 1000 mm and accounts for 80% of the total annual precipitation. The frostless period is as long as 6 months, the total

sunshine duration is as long as 1151 h, and the humidity is between 60% and 80% (Duan et al. 2020). The main forest vegetation types in Sejila Mountain are natural dark coniferous forests, with *A. georgei* var. *smithii* as the constructive species, as well as *Picea likiangensis* var. *linzhiensis*, mixed with *Sabina saltuaria*. Fir is the dominant tree species in the treeline community on shady and sunny slopes (Guo and Zhang 2015).

2.2 Sampling design

In July 2020, 12 large sample plots (100 m×100 m) were set at 100 m intervals within an altitude range of 3,800–4,400 m (Fig. 1). There were two series set in the northern and southern slopes of Sejila Mountain, respectively. Three 25 m × 25 m quadrats were set in each 100 m × 100 m plot, and each plot was not connected at different elevations. The basic information of the sampling plot is shown in Table 1. At each 25 m × 25 m quadrat, four 5 m × 5 m shrub survey quadrats and four 1 m × 1 m herb survey quadrats were set up to investigate the plant species,
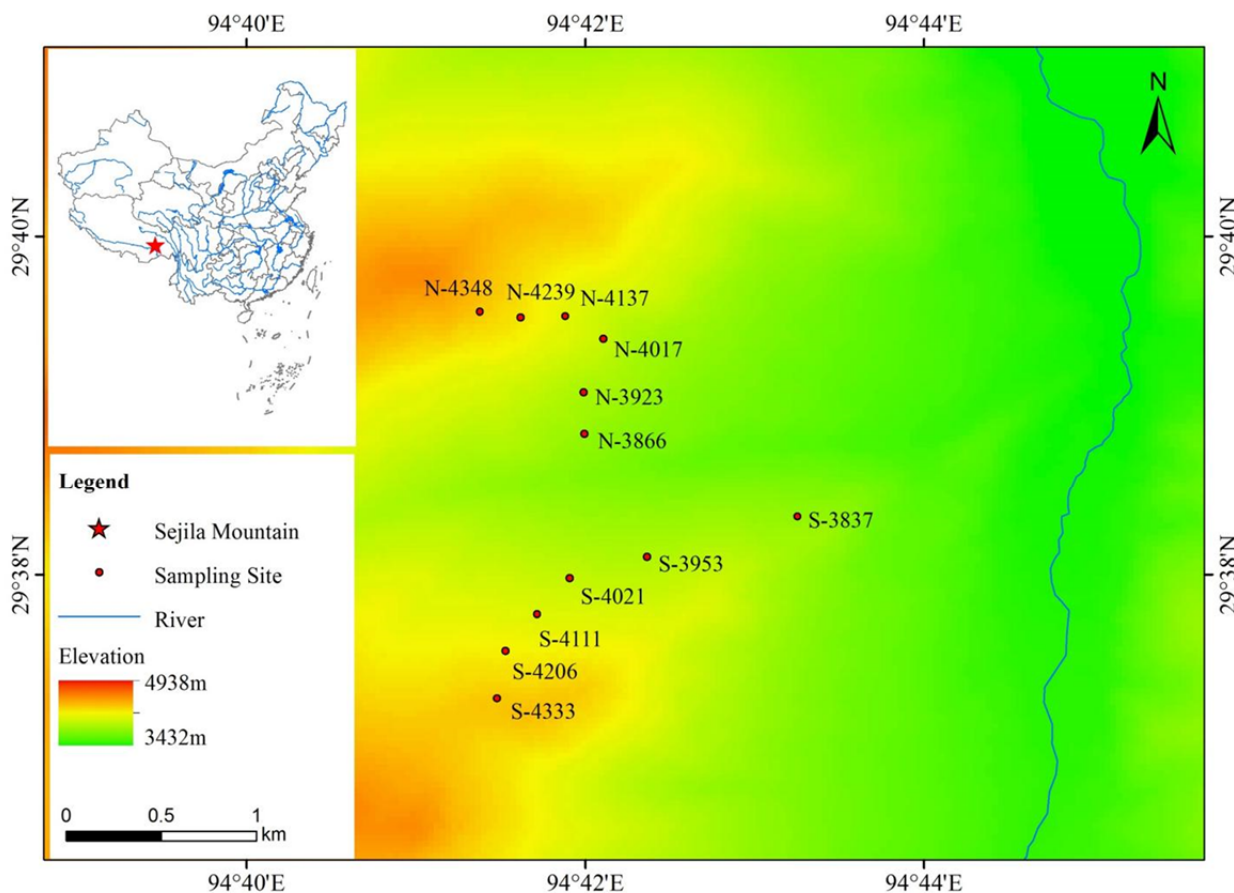

Fig. 1 Location of 12 sampling sites in Sejila Mountain.

average height, coverage, and other information of shrubs and herbs in each quadrat. (Table 1), and the species diversity index was calculated (Table 2). In each 25 m×25 m quadrats, the longest branch lengths of the arbor layer (diameter at breast height ≥ 5cm) were recorded. Crown width was calculated by the following formula: Crown width = (longest branch length from east to west × longest branch length from north to south)/2. Then, crown density (CD) was calculated as crown width divided by quadrats area (Wu et al. 2021). Herb coverage (HC) was the ratio of the vertical projected area of the aerial parts of herbs to the ground (Li et al. 2000).

A full excavation method (Willimas et al. 2019) was used to collect seedlings in every 25 m × 25 m quadrat. The Seedlings were divided into five age classes: 1–2, 3–4, 5–6, 7–8, and 9–10 years old. Seedlings were collected under unshaded conditions, and five plants of each age class were collected from each sample quadrat. Seedling age was determined by

branch color, floral, and bud scale markers (Duarte et al. 1999; Deng et al. 2018). Whole seedlings were dug out and marked. During the excavation of older seedlings, tools such as scrapers and brushes, were used to gently tap the roots along the lateral root extension until the root ends were obtained. This method can avoid the measurement error caused by other plant root interference and root damage.

At the same time of root collection, soil near seedling roots was also collected, and three soil samples (100–300 g) were collected from each 25 m × 25 m quadrat (a total of 108 soil samples). The soil profile near the seedling root was dug, and three samples of 0–20 cm of undisturbed soil were collected with cutting ring (100 cm3) from each quadrat (a total of 108 cutting ring samples).

2.3 Biomass measurements

The collected seedlings were divided into above-

Table 1 Basic information of the sampling plots in Sejila Mountain in Tibet.

Alt. (m)	Northern slope					Southern slope				
	Long. (°E)	Lat. (°N)	Average coverage	Average crown density	Litter thickness (cm)	Long. (°E)	Lat. (°N)	Average coverage	Average crown density	Litter thickness (cm)
3800	94.7111	29.6471	0.87±0.02	0.67±0.05	12.00±2.65	94.7212	29.6432	0.91±0.03	0.61±0.02	9.00±1.00
3900	94.7111	29.6490	0.66±0.04	0.52±0.03	9.00±1.73	94.7142	29.6413	0.78±0.02	0.67±0.02	13.00±4.00
4000	94.7120	29.6516	0.87±0.04	0.46±0.04	14.33±3.21	94.7105	29.6403	0.95±0.02	0.51±0.02	19.33±4.51
4100	94.7102	29.6527	0.86±0.04	0.61±0.03	10.33±2.52	94.7090	29.6385	0.87±0.02	0.45±0.04	15.33±2.52
4200	94.7081	29.6525	0.78±0.04	0.49±0.03	6.33±1.53	94.7074	29.6369	0.93±0.03	0.65±0.04	14.67±2.08
4300	94.7062	29.6529	0.69±0.04	0.46±0.02	14.67±3.06	94.7071	29.6346	0.71±0.03	0.41±0.02	17.67±4.51

Notes: Mean±Standard deviation (SD). Alt., Altitude; Long., Longitude; Lat., Latitude.

Table 2 Species diversity indices at different elevations on the northern and southern slopes of Sejila Mountain in Tibet

Alt. (m)	Species diversity on the northern slope							
	SG	SS	SSW	SP	HG	HS	HSW	HP
3800	3.33±0.58	0.55±0.10	0.94±0.21	0.78±0.11	5.00±1.00	0.58±0.12	1.13±0.28	0.70±0.10
3900	3.33±1.53	0.53±0.19	0.94±0.46	0.83±0.16	2.67±1.15	0.35±0.30	0.64±0.54	0.61±0.27
4000	5.00±1.00	0.13±0.05	0.34±0.11	0.21±0.05	4.67±0.58	0.59±0.20	1.15±0.37	0.76±0.25
4100	5.33±1.53	0.77±0.05	1.56±0.24	0.95±0.04	5.00±1.73	0.61±0.02	1.1±0.09	0.71±0.10
4200	2.00±0.00	0.40±0.14	0.59±0.15	0.84±0.22	1.33±0.58	0.13±0.22	0.19±0.32	0.27±0.47
4300	1	0	0	0	1	0	0	0
Alt (m)	Species diversity on the southern slope							
	SG	SS	SSW	SP	HG	HS	HSW	HP
3800	4.33±0.58	0.65±0.09	1.23±0.15	0.85±0.12	12.00±2.00	0.81±0.03	1.95±0.18	0.79±0.05
3900	5.33±2.31	0.70±0.14	1.44±0.48	0.88±0.09	6.33±1.53	0.61±0.14	1.23±0.30	0.68±0.17
4000	5.67±1.15	0.71±0.16	1.49±0.37	0.86±0.16	12.00±2.00	0.70±0.04	1.60±0.16	0.65±0.08
4100	4.00±0.00	0.64±0.09	1.20±0.24	0.87±0.17	7.00±1.73	0.76±0.04	1.57±0.19	0.82±0.04
4200	4.33±0.58	0.56±0.10	1.06±0.13	0.74±0.14	6.67±2.89	0.72±0.11	1.48±0.49	0.79±0.08
4300	5.00±1.00	0.71±0.05	1.38±0.18	0.87±0.02	6.67±2.08	0.71±0.08	1.45±0.28	0.77±0.06

Notes: Mean±Standard deviation (SD). SG: Shrub Gleason index; SS: Shrub Simpson index; SSW: Shrub Shannon–Wiener index; SP: Shrub Pielou evenness index; HG: Herbaceous Gleason index; HS: Herbaceous Simpson index; HSW: Herbaceous Shannon–Wiener index; HP: Herbaceous Pielou evenness index.

and below-ground parts. ABG is the sum of the stem, branch, and leaf biomass, and BGB is the sum of all root biomass. The seedlings were washed to remove the dust, soil and other impurities attached to the surface and then dried. During this process, damage to the seedlings was minimized, and the integrity of the ground and below-ground parts were ensured. The washed seedlings were inserted into envelopes and placed in an oven at 80°C to dry to constant mass, and then weighed (in grams).

2.4 Soil properties measurements

After removing stones and visible plant roots, the soil samples were sieved through a 0.25 mm screen. The physical and chemical properties of the soil samples were determined after air drying. Soil water content (SWC) was measured by drying method (Chang et al. 2012). Total organic carbon (TOC) was determined by the dry combustion method at 500°C (Storer et al. 1984). Total nitrogen (TN) and total phosphorus (TP) were determined by the Kjeldahl and NaOH alkali fusion molybdenum–antimony anti-colorimetric methods (Sparks et al. 1996), respectively. Total potassium (TK) and available potassium (AK) were determined by NaOH melt-flame photometry and 1 mol/L ammonium acetate extraction flame photometry (Gammon 1951), respectively. Available phosphorus (AP) was determined via an offline extraction column (Jakmunee and Junsomboon 2009). Nitrate nitrogen (NO_3^-–N) was determined by the phenol disulfonic acid colorimetry method (Haby 1989). Ammonium nitrogen (NH_4^+–N) was extracted with 1.2 mol/L KCl via the indophenol blue colorimetric method (Dorich and Nelson 1983). Particulate organic carbon (POC) was assayed according to the method of Garten et al. (1999). Easily oxidized organic carbon (EOC) was assessed according to the determination method of Chen et al. (2017). Dissolved organic carbon (DOC) was determined according to the method of Fang et al. (2014).

2.5 Biodiversity calculation

Gleason index (G), Shannon-Wiener index (SW), Simpson index (S), and Pielou evenness index (P) in α diversity were selected to measure plant richness, diversity, dominance, and distribution (Zhao et al. 2021). The calculation formulas are as follows:

Gleason index:

$$G = SN / \ln A \qquad (1)$$

Shannon–Wiener index:

$$SW = -\sum_{i=1}^{s} p_i \ln p_i \qquad (2)$$

Simpson index:

$$S = 1 - \sum_{i=1}^{s} p_i^2 \qquad (3)$$

Pielou evenness index:

$$P = H / H_{max}, \quad H_{max} = \ln SN, \qquad (4)$$

where A is the unit area; SN is the number of species; p_i is the relative frequency of each species; H_{max} is the maximum species diversity index, and $i=1, 2, 3, ..., n$.

2.6 Statistical analysis

Biomass allocation patterns were studied by logarithmically transformed allometric function with $\log_{10}$-transformed data (Ma and Wang 2020). The analyses for allometric scaling of AGB versus BGB were conducted separately for each age group of seedlings on biomass data. The allometric equation, $Y_1 = \beta Y_2^\alpha$, was used for univariate modeling, where Y_1 and Y_2 were BGB and AGB, respectively, and α and β are allometric coefficients. The equation was logarithmically transformed into the linear equivalent, $\log(Y_1) = \log(\beta) + \alpha \log(Y_2)$. A standardized major axis regression method (SMA) was used to calculate the exponential (α), 95% confidence interval (95%CI), determination coefficient (R^2) and the intercept $\log(\beta)$ of the regression mode in Soft Standardized Major Axis Tests and Routines (SMATR) (West et al. 1997; Niklas and Enquist 2001; Niklas 2004). The parameter α is the slope of linear regression after logarithmic power function, and $\log(\beta)$ is the intercept of linear regression.

The Kolmogorov-Smirnov test was used to determine whether all the biomass data had a normal distribution ($\alpha=0.05$).The relationship between AGB, BGB and seedling age at different elevations was determined by linear regression equation established by least square method. A mixed model ANOVA was used to assess the effect of elevation gradient (EG), slope aspect (SL) and seedling age (SA) on the AGB and BGB. The mathematical form: Biomass = elevation gradient (EG) + slope aspect (SL) + seedling age (SA) + elevation gradient (EG) × slope aspect (SL)

+ elevation gradient (EG) × seedling age (SA) + slope aspect (SL) × seedling age (SA) + elevation gradient (EG) × slope aspect (SL) × seedling age (SA) + (1| sampling point). Statistical analyses were conducted using Excel 2013 and the nlme package in R language (version 4.0.2). All charts depicting variations in parameters were generated using Origin 2021 (OriginLab, Northampton, MA ,USA).

The relationship between seedling biomass, soil properties and vegetation factors was investigated by redundancy analysis (RDA)-constrained ranking of experimental data using Canoco 5.0 (Microcomputer Power, Ithaca, NY, USA). RDA analysis has two matrices: species data, which include AGB and BGB, and environmental data, which consist of soil properties (SWC, TOC, TN, TP, TK, AK, AP, NO_3^--N, NH_4^+-N, POC, EOC, DOC) and stand factors (HC, CD, LT, SG, SS, SSW, SP, HG, HS, HSW, HP). In addition, the variation decomposition method was used to quantify the individual and joint explanations of stand and soil factors for *A. georgei* var. *smithii* seedling biomass. Variation decomposition was analyzed using the vegan package in R language (version 4.0.2).

3 Results

3.1 Variation of the AGB and BGB of *A. georgei* var. *smithii* seedlings in different slope aspects, altitudes, and seedling ages

AGB and BGB increased with seedling age, and most of the biomass was concentrated in the above-ground part (Fig. 2). The results from a mixed model ANOVA revealed that (Table 3), SA had significant effects on the AGB and BGB of *A. georgei* var. *smithii* seedlings ($p<0.001$), but slope aspect (SL) and elevation gradient (EG) had no significant individual effects ($p>0.05$). The interactive effects of SL and EG (i.e., SL×EG) had significant effect on AGB ($p<0.05$), SL×SA and SL×EG×SA had extremely significant effect on AGB ($p<0.001$), but EG×SA had no significant effect on AGB ($p>0.05$). SL×EG, SL×SA, EG×SA, and SL×EG×SA had no significant effect on BGB ($p>0.05$).

Regression analysis was conducted on the relationship between seedling age and biomass of *A. georgei* var. *smithii* seedlings (Appendix 1). The results showed that AGB and BGB at different altitudes on the two slope aspects showed a binomial

Table 3 Results from a mixed model ANOVA investigating the influence of elevation gradient, slope aspect and seedling age on AGB and BGB in *A. georgei* var. *smithii* seedlings.

Biomass	Factors	DF	*F*-value	*p*-value
AGB	SL	1	0.14	0.707
	EG	5	1.36	0.243
	SA	4	212.70	<0.001
	SL×EG	5	2.62	0.027
	SL×SA	4	5.68	<0.001
	EG×SA	20	0.70	0.821
	SL×EG×SA	20	3.23	<0.001
BGB	SL	1	0.09	0.761
	EG	5	0.67	0.649
	SA	4	101.10	<0.001
	SL×EG	5	0.87	0.504
	SL×SA	4	0.67	0.613
	EG×SA	20	0.71	0.809
	SL×EG×SA	20	1.37	0.151

Notes: AGB: Above-ground biomass; BGB: Below-ground biomass; SA: Seedling age; EG: Elevation gradient; SL: Slope aspect; DF: Degree of freedom.

growth trend with the increase in seedling age. The fitting degree between AGB and seedling age was the highest at 4000 m (R^2=0.921) on the northern slope and the lowest at 4100 m on the southern slope (R^2=0.544). The fitting degree between BGB and seedling age was the highest at 4100 m (R^2=0.938) on the northern slope and the lowest at 4100 m (R^2= 0.483) on the southern slope. The slope of AGB regression equation was higher than that of BGB regression equation at the same elevation on both slope aspects, which indicates that the accumulation rate of AGB was higher than that of BGB with the increase in seedling age.

3.2 Allometric relationship between AGB and BGB of A. georgei var. smithii seedlings

The linear relationship of the log₁₀-transformed biomass data was used to represent the biomass allocation patterns of *A. georgei* var. *smithii* seedlings. An allometric relationship existed between AGB and BGB at different elevations on both slope aspects ($\alpha \neq 1$, Fig. 3, Fig. 4). The test of allometry shows that (Appendix 2), AGB and BGB showed an isometry relationship at 4000 m, 4100 m, 4200 and 4300 m on the north slope (allometric exponential α has no

significant difference with 1), and showed allometric relationship at other two elevations; at 3800 m, 3900 m and 4000 m on the southern slope, AGB and BGB showed isometric relationship (allometric exponential *α* was not significantly different from 1), and the other three altitudes showed allometric relationship between AGB and BGB. The allometric exponential between AGB and BGB on the northern slope was the lowest at 3800 m (95%CI: 0.810–1.015) (Fig. 3A) and the highest at 4300 m (95%CI: 0.968–1.123, Fig. 3F). R^2 varied from 0.884 to 0.989 (Fig. 3). On the southern slope, the allometric growth index between AGB and BGB ranged from 1.004 to 1.268 (Fig. 4), the lowest was at 4000 m (95%CI: 0.827–1.181, Fig. 4C), the highest was at 4100 m (95%CI: 1.054–1.483, Fig. 4D), and R^2 varied from 0.912 to 0.959 (Fig. 4). In conclusion, *A. georgei* var. *smithii* seedlings shared internal commonality in biomass allocation in different slope aspects and altitudes.

3.3 Environmental factors affecting biomass of *A. georgei* var. smithii seedlings

Trend correspondence analysis (DCA) was performed on the species data (AGB and BGB), and the four ranking axes of the species data were all less than 3. Therefore, linear

Fig. 2 Variation of the biomass of *A. georgei* var. *smithii* seedlings at different elevations and slope aspects in Sejila Mountain in Tibet. Error bars indicate the standard error.

model RDA was selected. The RDA results showed that in the northern slope, the cumulative contribution rate of soil factors to the first two axes of
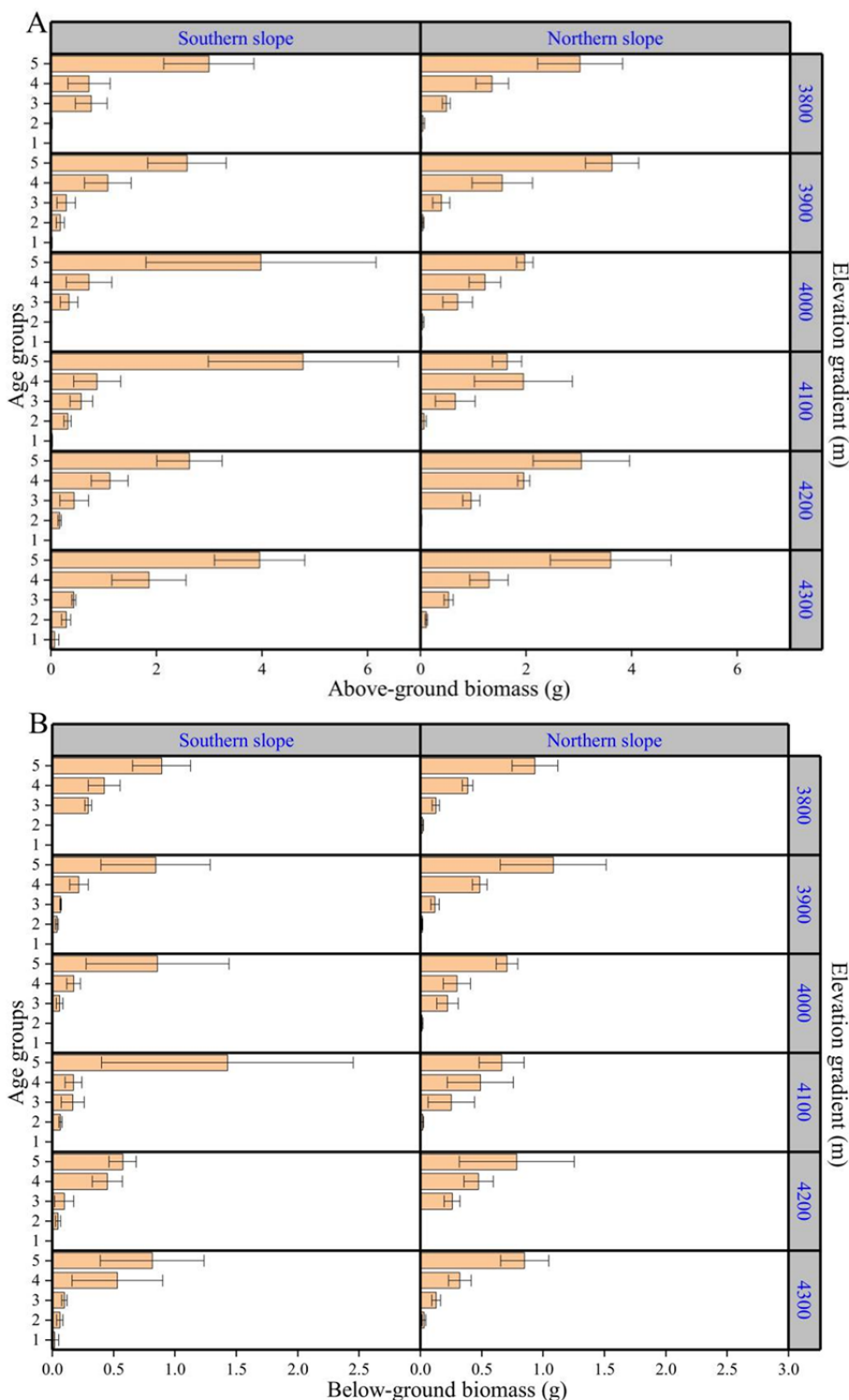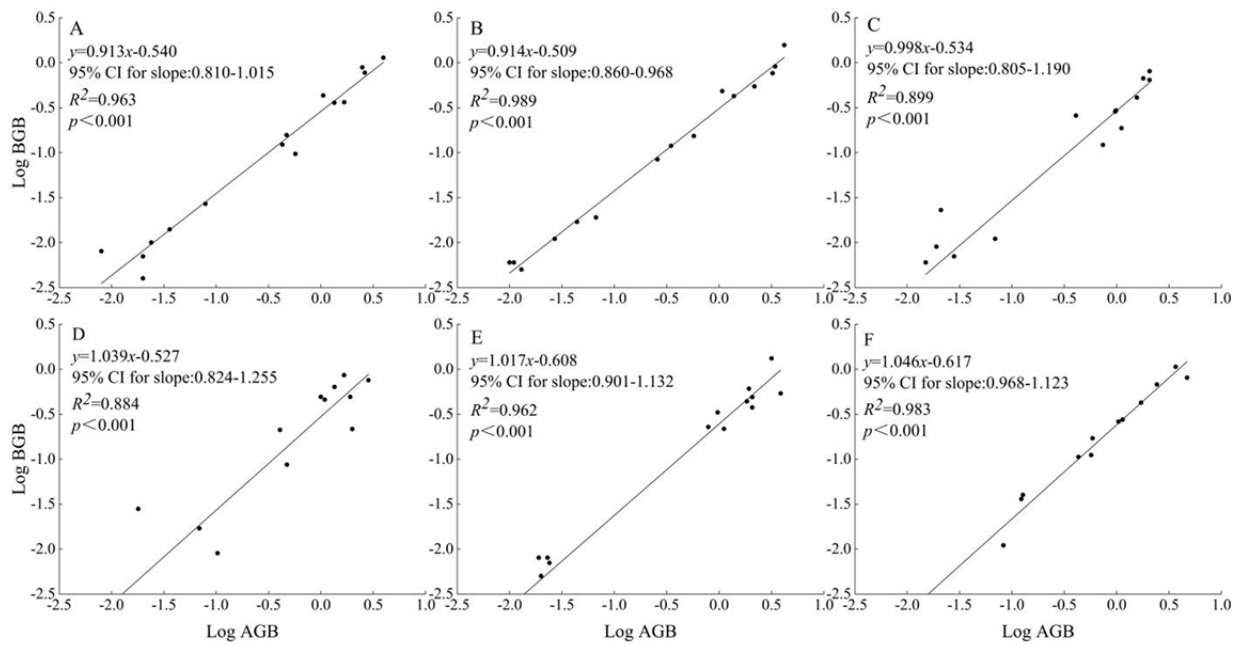
Fig. 3 Allometric relationship between the above-ground biomass (AGB) and below-ground biomass (BGB) of *A. georgei* var. *smithii* seedlings at different elevations (A: 3800 m; B: 3900 m; C: 4000 m; D: 4100 m; E: 4200 m; F: 4300 m) on the northern slope.
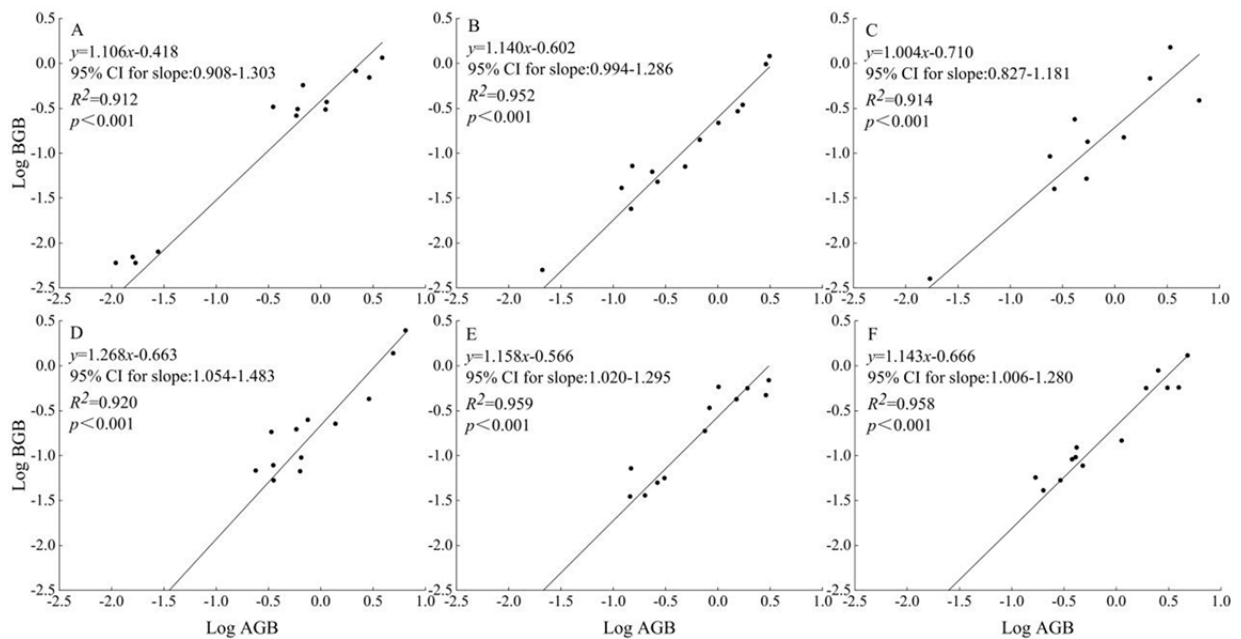

Fig. 4 Allometric relationship between the above-ground biomass (AGB) and below-ground biomass (BGB) of *A. georgei* var. *smithii* seedlings at different elevations (A: 3800 m; B: 3900 m; C: 4000 m; D: 4100 m; E: 4200 m; F: 4300 m) on the southern slope.

AGB and BGB was 90%, and that of stand factors to the first two axes of AGB and BGB was 92.69% (Appendix 3). On the southern slope, the cumulative contribution rate of soil factors to the first two axes of AGB and BGB was 90.36%, and that of stand factors to the first two axes of AGB and BGB was 90.19%

(Appendix 3). Therefore, the first two ordination axes of RDA can be used to reflect the effects of soil and stand factors on the AGB and BGB of *A. georgei* var. *smithii* seedlings with different seedling ages (Fig. 5).

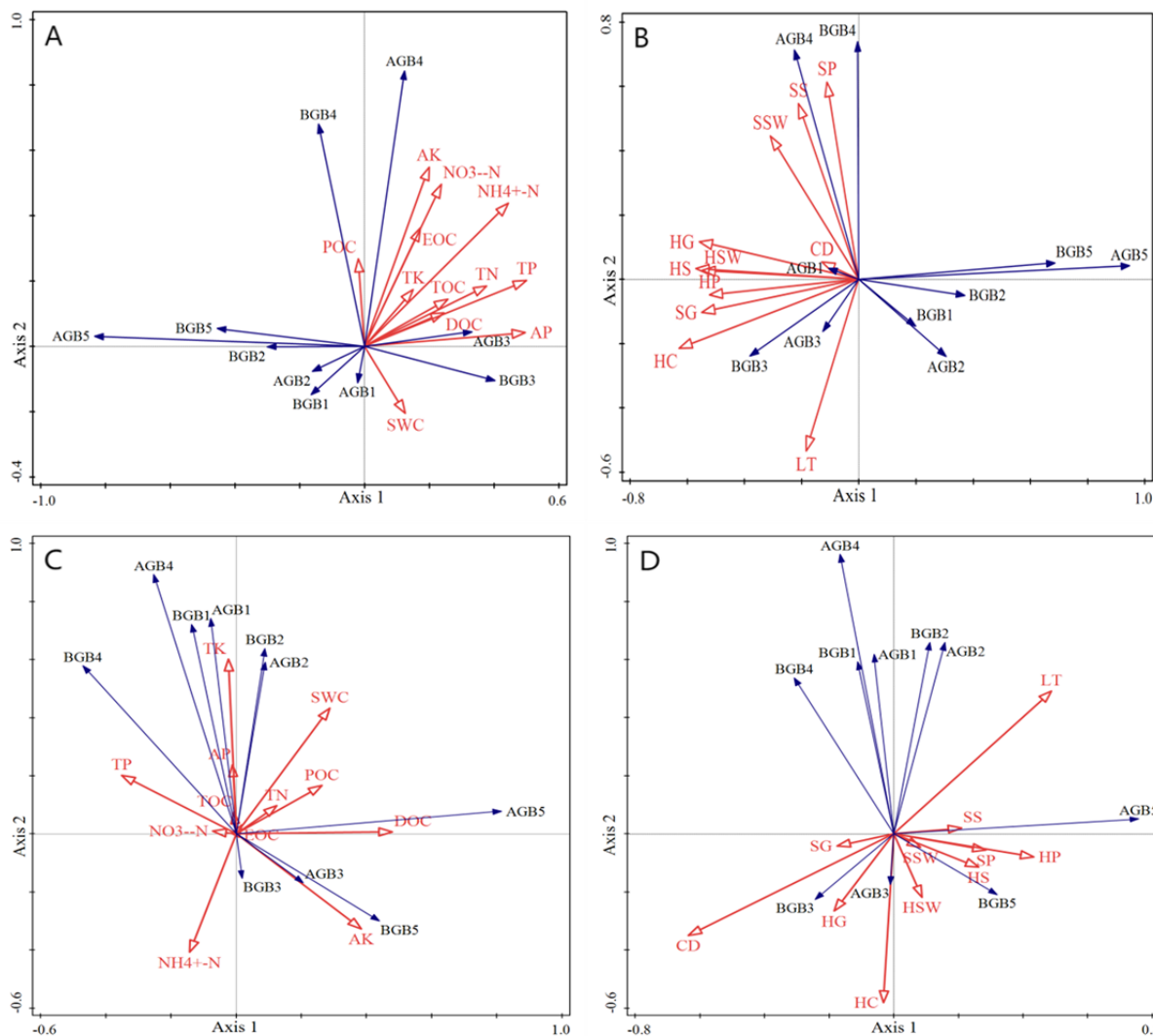The line length of the arrow represents the degree of effect of environmental factor on the AGB and BGB

Fig. 5 Redundancy Analysis (RDA) double-sequence diagram of soil factors, plant community characteristics, and biomass of *A. georgei* var. *smithii* seedlings at different age groups on the northern (A, B) and southern slope (C,D). The length of the vector represents the intensity of impact, arrows in the same direction have positive correlation, arrows of the opposite direction have negative correlation, the red line indicates environmental factors, and the blue line indicates species factors. AGB1, AGB2, AGB3, AGB4, AGB5 and BGB1, BGB2, BGB3, BGB4, BGB5 are the above-ground biomass and below-ground biomass for the 1-2, 3-4, 5-6, 7-8, 9-10 year-old seedlings, respectively. The full name of the abbreviation on the figure was shown in Appendix 4.

of *A. georgei* var. *smithii* seedlings with different seedling ages. A longer line represents a greater influence, vice versa. On the northern slope, the arrow lines of AK, NO$_3^-$−N, NH$_4^+$−N, TP, and AP were long (Fig. 5A), and the arrow lines of CD was short (Fig. 5B), which indicated that the AGB and BGB of *A. georgei* var. *smithii* seedlings were more affected by stand factors. On the southern slope, the arrow lines of TK, AK, SWC, DOC, NH$_4^+$−N, and TP were longer (Fig. 5C), and the arrow lines of stand factors, LT, CD, and HC were longer (Fig. 5D), which indicated that the AGB and BGB of *A. georgei* var. *smithii* seedlings

were more affected by soil factors. On the northern slope, soil factors were negatively correlated with AGB and BGB (Fig. 5A), and stand factors were positively correlated with AGB and BGB (Fig. 5B). On the southern slope, soil factors were positively correlated with AGB and BGB (Fig. 5C), and stand factors were negatively correlated with AGB and BGB (Fig. 5D).

We adopted the method of variation decomposition to carry out the forward selection of explanatory variables for stand and soil factors to further quantify their individual and interactive effects. On the northern slope, the contribution of

stand factors to AGB and BGB accounted for 47.8%, and soil factors contributed lesser at 21.5%. The common explanation rate of the two environmental groups to seedlings' biomass accounted for 12.2% (Fig. 6A). However, on the southern slope, the contribution of stand factors to AGB and BGB accounted for only 20.5%. Soil factors contributed more to biomass at 53.2%. The common explanation rate of the two environmental groups to seedlings' biomass accounted for 10.7% (Fig. 6B).
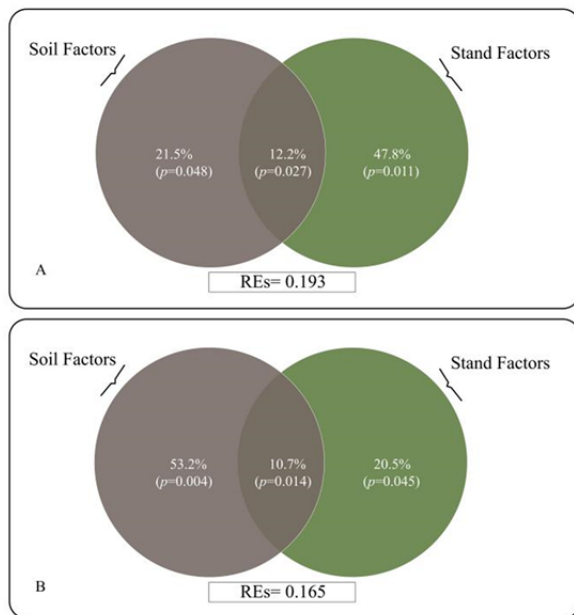

Fig. 6 Venn diagram of the explanatory rates of soil and plant community characteristics on biomass of A. georgei var. smithii seedling on the northern (A) and southern slope (B). The overlapping part is the common explanation rate of soil and plant community characteristics to seedlings biomass. REs means residuals, which indicate a part of the unexplained change.

4 Discussion

Topographic conditions (including slope aspect, elevation, slope position, etc.) are considered important factors affecting plant biomass in subtropical regions (Alves et al. 2010; Sato 2010; Lin et al. 2012). Slope aspect affects biomass indirectly by changing litter decomposition and soil nutrient cycling rate (Hicks and Frank 1984; Thakur et al. 2019). The present study showed that the AGB and BGB between the northern and southern slopes had no significant difference ($p>0.05$; Fig. 2, Table 3),

which indicated that the individual effect of slope aspect (SL) on biomass was weak. However, when SL interacted with SA and EG (SL×EG, SL×SA, SL×EG×SA), the AGB of *A. georgei* var. *smithii* seedlings was significantly affected ($p<0.05$, Table 3), which indicated that slope aspect had a strong indirect combined effect on biomass and was consist with previous studies. Canadell et al. (1988) studied the biomass of *Quercus ilex* L. on the northern and southern slopes and found that the allometric exponential of the northern and southern slopes are 1.544 ($R^2=0.775$) and 2.077 ($R^2=0.840$), respectively; the allometric equations of biomass on the southern and northern slopes were significantly different ($p<0.05$); and slope aspect has a significant effect on biomass ($p<0.05$). Wang et al. (2014) found the average biomass of *Abies georgei.* on the northern slope is 16.639 g higher than that on the southern slope (11.397 g). The differences may be due to the spatial heterogeneity of the ecosystem caused by the slight differences in topography and soil characteristics (Nie et al. 2019).

Elevation controls plant growth and ecosystem function through indirect changes to other drivers such as soil properties, species diversity et al. (Fu et al. 2020; Case and Peterson 2005). We found that elevation had no significant effect on the AGB and BGB ($p>0.05$), but the interactive effects of EG, SL, and SA (i.e., SL×EG, SL×EG×SA) had a significant effect on the AGB of *A. georgei* var. *smithii* seedlings ($p<0.05$, Table 3). Hertel and Schling (2011) found that *Picea asperata* biomass increases considerably with elevation in the Alps, and the biomass of *P. asperata* at the highest elevation was almost twice more than that at the lowest altitude. In the central Himalayas of India, the average biomass of *Celtis australis* seedlings at low EG (550−1000 m), middle EG (1050−1250 m) and high EG (1350−1980 m) were respectively 8.4±2.5 g, 9.4±3.3 g, and 12.7±1.7 g, and EG has a significant effect on biomass ($p<0.01$)(Singh et al. 2006), which were different from our results. The difference may be due to the fact that the longitude and altitude gradients in plant biomass are associated with pervasive geographic patterns in the structure and function of forest ecosystems (e.g., forest biodiversity, soil chemical characters, vegetation primary production, etc.) (Han et al. 2011). Therefore, we analyzed the effects of soil and stand factors on the AGB and BGB of *A. georgei* var. *smithii* seedlings and explained them in detail in the

following discussion.

Optimal allocation theory holds that plants should adapt to environmental changes by investing more biomass in the various organs that receive the most limited resources (Zhang et al. 2011). Biomass allocation patterns might reflect the self-coordinating mechanism of plants that maximizes resource utilization (Li et al. 2017). In the present study, the allometric exponential α of the relationship between BGB and AGB of *A. georgei* var. *smithii* seedlings were larger at higher elevations (Fig. 3, Fig. 4). This result suggests that *A. georgei* var. *smithii* seedlings at high elevations increased their allocation to BGB, because water is the main limiting factor for plant growth at high elevations (Peichl and Arain 2007; Weiner 2004). The hydrothermal conditions at low altitudes are relatively favorable for plant growth, but plant growth at high altitudes is limited by low temperatures (Zheng et al. 2004). Thus, *A. georgei* var. *smithii* seedlings increased their investment to underground parts to meet the nutrient and water transport requirements at high altitudes.

The allocation of biomass by seedling ages follows the principle of balance between plant growth and resource allocation among plant components, and its purpose is to maintain the normal physiological activities and functions of plant components (Landsberg and Sands 2011; Mensah et al. 2016). We found that the AGB and BGB of *A. georgei* var. *smithii* seedlings were significantly affected by seedling age ($p<0.001$, Table 3), and the accumulation rate of AGB was greater than that of BGB with the increase in seedling age (Appendix 1). Some studies also found that with the growth of seedling, the above-ground part grows larger because of individual changes; more resources are allocated to above-ground growth; and the accumulation rate of AGB is higher than that of BGB (Mensah et al. 2016).

In the early 1970s, some researchers studied the relationship between seedling age and biomass through allometric equation, and the fitting regression coefficient of the allometric equation was depended on the composition and plant species (Bond-Lamberty et al. 2002; Saint-André et al. 2005). In the present study, we found that the AGB and BGB accumulation of *A. georgei* var. *smithii* seedlings had obvious gradient with the increasing of age class; therefore, we established the allometric equation of biomass to predict the changes in the biomass and carbon storage of *A. georgei* var. *smithii* seedlings (Fig. 3, Fig. 4). The

regression analysis of log10 biomass data showed that the allometric exponential between AGB and BGB was 0.913–1.268 (95%CI: 0.810–1.483), which was close to $\alpha=1$, following the isometric distribution hypothesis (Enquist and Niklas 2002; Niklas 2005, 2006). This value was close to the allometric exponential between the AGB and BGB of China plant (1.04 [95%CI: 1.00–1.08]) (Cheng and Niklas 2007) and between the AGB and BGB of global plant (1.09 [95%CI: 1.05–1.13]) (Enquist and Niklas 2002). However, the allometric exponential of *A. georgei* var. *smithii* seedlings in present study was different from that of boreal/alpine *Picea–Abies* forest 0.67(95%CI: 0.61–0.73) (Zhang et al. 2016). The intercept ($\log(\beta)$: −0.710 to −0.418) of the allometric growth of *A. georgei* var. *Smithii* seedlings was also different from that of Chinese vegetation ($\log(\beta)$: 0.366), global vegetation ($\log(\beta)$: 2.59), and boreal/alpine *Picea–Abies* forest ($\log(\beta)$: 0.06). The absolute values of the AGBs of different vegetation types were remarkably different from those of BGBs (Cheng and Niklas 2007).

Many studies analyzed the relationship between plant community characteristics (canopy density, litter, species diversity, etc.) and plant biomass. These studies found that the shading effect produced by canopy density affect solar radiation and weaken plant photosynthesis (Comeau et al. 1993; Perrin and Mitchell 2013); litter inhibits seedling colonization by reducing available water and acting as a mechanical barrier (Caccia and Ballaré 1998; Maruyama et al. 2004); and the interspecific competition of species diversity has a remarkable effect on seedling growth and biomass (Gerlach et al. 1997; Yann et al. 2018). Our study found that the contribution rate of stand factors to the AGB and BGB of *A. georgei* var. *smithii* seedlings was higher on the northern slope (47.8%) but lower on the southern slope (20.5%, Fig. 6), which indicated that canopy density (CD), litter thickness (LT), species diversity, and other factors were highly correlated with the biomass of *A. georgei* var. *Smithii* seedlings on the northern slope. RDA also confirmed this point. Except for CD, the correlation between the other plant community characteristics and biomass were all long on the northern slope (Fig. 5B), which indicated that the plant community characteristics on the northern slope were more suitable for the growth of *A. georgei* var. *smithii* seedlings. However, the reason for the lower contribution rate of the stand factors in the southern slope may be that the growth and development of seedlings were inhibited by

higher canopy density, litter thickness, and species diversity index (Appendixes 1, 2).

The contribution rate of soil factors to the AGB and BGB of *A. georgei* var. *smithii* seedlings was higher on the southern slope (53.2%) and lower on the northern slope (21.5%, Fig. 6), which indicated that soil nutrients, SWC, and other factors on the southern slope were highly correlated with the biomass of *A. georgei* var. *smithii* seedlings. Fig. 5C showed that the correlation between TK, AK, SWC, DOC, NH_4^+-N, TP and biomass in the southern slope was greater than that in the northern slope, which indicated that the soil condition on the southern slope was more suitable for the growth of *A. georgei* var. *smithii* seedlings. Some studies found that the spatial distribution of soil properties was affected by slope aspect, slope steepness, and slope position (Castilho et al. 2006; Nie et al. 2019). Soil characteristics in the northern and western slopes had higher soil nutrient content than those in the southern and eastern slopes, and soil factors had a higher impact on biomass in the northern slope (Nie et al. 2019), which was inconsistent with our research results. The cause may have to do with the presence of vegetation on the ground, and the complex vegetation distribution may change the negative correlation between slope aspect and soil nutrients (Nie et al. 2019). In addition, studies found that because the northern slope has more dense vegetation coverage, it retained more soil water; thus, it had more biomass (Yetemen et al. 2015). Notably, in the present study, the southern slope had denser vegetation coverage and greater soil moisture retention, but stand factor is negatively

correlated with seedling biomass (Fig. 5D), which seriously inhibits the growth of the seedlings. This result was also consistent with our previous discussion on the effects of stand factors on the biomass of *A. georgei* var. *smithii* seedlings on the southern slope.

5 Conclusions

Seeding age is an important factor affecting the biomass of *A. georgei* var. *smithii* seedlings in Southeast Tibet, and AGB and BGB increased with increasing seedling age. The analyses for allometric relationship between BGB and AGB appeared to be a useful tool to provide an accurate description of the biomass allocation patterns of *A. georgei* var. *smithii* seedlings. In sub-alpine ecosystems, *A. georgei* var. *smithii* seedlings increased BGB input in order to adapt to high-altitude habitats. Our results confirmed that allometric theory and optimal allocation theory are complementary in explaining biomass allocation. Moreover, the biomass of seedlings was affected differently by environmental factors on both slopes. The biomass of *A. georgei* var. *Smithii* seedlings on the northern slope was greatly affected by plant community characteristics, whereas soil priority was the dominant factor on the southern slope. By exploring the biomass allocation mechanism of *A. georgei* var. *smithii* seedlings and their relationship with habitat conditions, the present study provided evidences of the survival strategies of *A. georgei* var. *smithii* seedlings at high altitudes in Tibet plateau.

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