

RESPONSES OF ROOT GROWTH AND FINE ROOT BIOMASS OF *ABIES GEORGEI* VAR. *SMITHII* SEEDLINGS OF DIFFERENT AGE LEVELS TO ENVIRONMENT IN SOUTHEAST TIBET

ZHANG, X. S. – LU, J. * – ZHOU, C. N. – ZHANG, M. – YU, D. S.

*Institute of Tibet Plateau Ecology, Tibet Agricultural & Animal Husbandry University,
Nyingchi, Tibet 860000, China*

*Key Laboratory of Forest Ecology in Tibet Plateau (Tibet Agricultural & Animal Husbandry
University), Ministry of Education, Nyingchi, Tibet 860000, China*

*Linzhi National Forest Ecosystem Observation & Research Station of Tibet, Nyingchi, Tibet
860000, China*

Key Laboratory of Alpine Vegetation Ecological Security in Tibet, Nyingchi, Tibet 860000, China

**Corresponding author
e-mail: tibetlj@163.com*

(Received 19th Apr 2022; accepted 11th Jul 2022)

Abstract. The root distribution of most plants at high elevations in the soil is vague because studying roots at different elevations is time consuming and methodologically challenging. The purpose of this study is to understand the growth characteristics of the seedling roots of different age groups of *Abies georgei* var. *smithii* along the elevation bands in Southeast Tibet, as well as the influence of environmental factors on the growth of seedling roots. In July 2021, the roots of seedlings of five age classes were collected from six elevation bands (3800, 3900, 4000, 4100, 4200, and 4300 m) on the western slope of Sejila Mountain in southeastern Tibet. Rhizosphere soil sampling and analysis were conducted to assess the influence of elevation on the distribution characteristics of seedling root growth and fine root biomass (FRB), and the correlations of these characteristics with various soil factors were studied. Results showed that no significant differences in root length and FRB were observed among different elevation bands ($p > 0.05$), but significant differences among different age groups were noted ($p < 0.05$). Root length and FRB remarkably increased with increasing age class. Ammonium nitrogen and particulate organic carbon were the main soil factors affecting the root growth of seedlings, and available phosphorus was the major contributor to the FRB. In summary, soil factors play an important role in *A. georgei* var. *Smithii* seedlings' root growth at high elevation areas.

Keywords: *root distribution, age level, elevation, soil properties, seedling*

Introduction

In the gradient study of plant adaptation to environmental characteristics, elevation gradient gradually replaced latitudinal gradient as the model template (Rahbek, 2005). Elevation and environmental changes related to elevation (climate, soil factors, etc.) can induce plants to produce corresponding traits, thus directly or indirectly controlling local ecosystem processes (Violle et al., 2007; Paillex et al., 2013). Studies have shown that the growth of species at high elevation is limited by climate severity and resource availability (Lomolino, 2010). Among them, soil nutrients, as important resources for plant growth and development, vary significantly at different elevations (Wilcox and Nichols, 2008). Consequently, elevation gradient is a suitable natural platform for exploring the effects of environmental factors on plant roots (Dunne et al., 2004; Malhiet al., 2010).

As a part of the natural ecosystem, the root system not only participates in numerous ecological processes (Jackson et al., 1990; Eissenstat, 1992; Norby et al., 2000; Bardgett et al., 2014) but also provides various ecological benefits for the underground and above-ground environments (Thevathasan and Gordon, 2004; Jose, 2009; Ramachandran et al., 2009). Root distribution refers to the distribution and growth pattern of roots in soil, which can be divided into horizontal roots distribution and vertical roots distribution (Qi, 2020). Information on the distribution of plant roots is the basis for understanding the underground ecological processes of plants (Mandy et al., 2011). Because of the spatial heterogeneity of environmental factors at different scales, root distributions are largely influenced by environmental factors, such as topography, climate, and soil (Schenk and Jackson, 2005), and their response to environmental factors is plastic (Simpson et al., 2020; Gonzalez-Ollauri et al., 2021). Previous studies attempted to analyze the relationship between root distribution and environmental factors, and results showed that, compared with other factors, root distribution is mostly determined by soil factors and tree age (Chang et al., 2012; Zhang et al., 2018).

The underground biomass, including coarse and fine roots, is an important component of the total biomass of woodland ecosystems (Qi et al., 2019); by comparison, fine roots (diameter < 2 mm) play an important role in the dynamics of water, nutrients, and carbon in the ecosystem (Zhang et al., 2018). Therefore, temporal and spatial changes in fine root biomass (FRB) and its distribution patterns have been extensively studied (Ronald and Hendrick, 1993; Yuan and Chen, 2010; Li et al., 2019; Xu et al., 2019). The growth of fine roots is relatively independent of stem growth, and spatiotemporal changes in root growth largely depend on soil conditions (Makkonen and Helmisaari, 2001). Earlier studies revealed that the biomass of fine roots along elevation gradient is generally determined by soil temperature and humidity (Foster et al., 2020) and increases with tree age (Makkonen and Helmisaari, 2001). Previous research on plant root biomass in high-elevation areas in China mainly focused on the Loess Plateau, Inner Mongolia Plateau, and Qinghai-Tibet Plateau; studies on the FRB at a certain elevation have also been conducted (Qi et al., 2020; Ma et al., 2008; Wang et al., 2007). Unfortunately, changes in FRB with the elevation gradient and tree age have not been explored.

Studies have shown that both root distribution and root biomass belong to the category of root traits (Li et al., 2016; King, 2021). Although some researchers have found that root traits played an important role in competition dynamics and stress tolerance (Leger et al., 2019; Bristiel et al., 2019; Kramer-Walter et al., 2016; Markesteijn and Poorter, 2009), but so far, most studies just focused on aboveground. Until recently, studies have linked root traits to seedling establishment and survival. For example, changes in seedling root length explained most of the changes in seedling survival (Harrison and LaForgia, 2019) and were the best predictors of seedling survival in wild sites (Leger et al., 2019). Root mass ratio was correlated with seedling competitiveness (Ferguson et al., 2015; Leger and Goergen, 2017); There was a trade-off between root dry matter content and growth rate (Larson et al., 2020). Other studies have found that some characteristics of roots were closely related to soil nutrients and water content (Kramer-Walter et al., 2016; Bristiel et al., 2019; Hanslin et al., 2019). However, these studies did not pay attention to the effects of elevation, age grade and soil factors on root traits. Under the background of ecological security stress on the Qinghai-Tibet Plateau, it is urgent to study the effects of environment (elevation, soil and other factors) on plant survival and the ecological strategies of plants.

Sejila Mountain in Southeast Tibet is well known for its extensive forest coverage and pivotal role as an ecological security barrier (Kato et al., 2006). The mountain coverage is mainly composed of dark coniferous forest, in which *Abies georgei* var. *smithii* is the dominant species. Research on the seedlings of *A. georgei* var. *smithii* in Sejila Mountain mainly focus on their spatial pattern and natural regeneration (Luo, 2010; Xie et al., 2015; Wang et al., 2018); however, the elevation distribution of the root growth of these seedlings and its relationship with soil factors remains unclear. Therefore, in this study, we selected different ages of *A. georgei* var. *smithii* seedlings to explore the growth and distribution characteristics of their root system along elevation bands, as well as their relationships with environmental factors. The results of this work will provide theoretical support and basic data for the protection of subalpine forest resources on the Qinghai–Tibet Plateau and boost the subalpine forest system play an excellent ecological security barrier function. The objectives of the present study were as follows: (i) investigate the distribution characteristics of horizontal root lengths (HRL), vertical root lengths (VRL), fine root biomass (FRB) of *Abies georgei* var. *smithii* seedlings along different elevations; (ii) investigate the variation of horizontal root lengths (HRL), vertical root lengths (VRL), fine root biomass (FRB) of *Abies georgei* var. *smithii* seedlings at different age levels; (iii) explore the individual effect and interaction of elevation and age level on root length and FRB; (iv) sort out the main soil influencing factors of root length and FRB.

Materials and methods

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 of China (Fig. 1). Sejila Mountain is close to the branch of the Yarlung Zangbo River (Niyang River basin), with an elevation of 2100–5300 m, and is part of the Nyenqing Tanggula mountain range (Zhou et al., 2015). This region is characterized by typical warm temperate and temperate mountain climates, with dry and wet seasons. The annual temperature ranges from –13.98 °C to 9.23 °C, and the annual average temperature is –0.73 °C (Wang et al., 2019). Most of the rainfall occurs from June to September, and the precipitation could exceed 1000 mm, accounting for 80% of the total precipitation received by the area annually. The frost 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).

Sample collection

In July 2017, a 50 m × 50 m plot were established at elevations of 3800, 3900, 4000, 4100, 4200, and 4300 m. The plot was not connected to each other at different elevations, and a total of 6 plots were established. The basic information of plots at each elevation are shown in Table 1.

The whole excavation method (Williams et al., 2019) was used to collect all seedlings of *A. georgei* var. *smithii* in each plot. The collected seedlings were divided into five age grades: 1–2 years old, 3–4 years old, 5–6 years old, 7–8 years old, and 9–10 years old; here, 5 seedlings of each age grade were collected from each plot. Seedling age was determined by branch color, lenticels, and bud scale marks (Parent et al., 2003). The age of the seedlings was determined according to the following method. Starting from the top

of the branches and extending to the base of the seedlings, the branches of the current year can be identified as the 1-year-old branches; then downwards, according to the bud scale marks and the color of the branches, 2-10 years old branches were determined. At last, the number of annual rings at the base of the branches were used to verify the age levels (Deng et al., 2018). During excavation, roots were gently dipped along the lateral root extension direction by using tools such as a spatula and brush until the end of the root system was obtained. This method could help avoid measurement errors due to the interference of other plants' roots and seedling root damage.

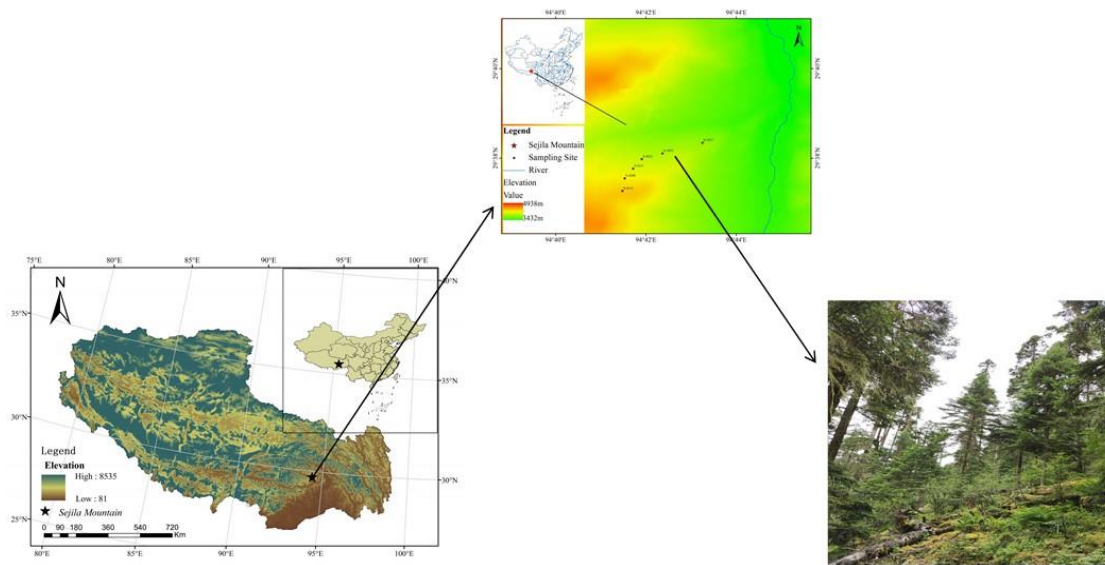


Figure 1. Study area, sampling sites and habitats

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 plot (a total of 18 soil samples). The soil profile near the seedling root was dug, and three samples of 0–20 cm of undisturbed soil was collected with cutting ring (100 cm³) from each plot (a total of 18 cutting ring samples). The collected soil samples were stored in plastic bags at a low temperature and promptly sent to the laboratory for processing. Soil temperature (ST) were measured by a portable soil hygograph (KM-WSD01, Jingmai Instruments Inc, China). Please refer to *Table A1* in the supplementary document for soil index data.

Table 1. Basic situation of the sample site

Elevation (m)	Longitude (°E)	Latitude (°N)	Slope angle (°)	Slope aspect	Average coverage	Average crown density	Main species
3837	94.7212	29.6432	24	South	0.91 ± 0.03	0.61 ± 0.02	<i>LoniceraInconspicua</i> ; <i>Abies georgei</i> var. <i>smithii</i>
3953	94.7142	29.6413	36	South	0.78 ± 0.02	0.67 ± 0.02	<i>LoniceraInconspicua</i> ; <i>Abies georgei</i> var. <i>smithii</i>
4021	94.7105	29.6403	39	South	0.95 ± 0.02	0.51 ± 0.02	Bryophyte; <i>Abies georgei</i> var. <i>smithii</i>
4111	94.7090	29.6385	36	South	0.87 ± 0.02	0.45 ± 0.04	Bryophyte; <i>Abies georgei</i> var. <i>smithii</i>
4206	94.7074	29.6369	36	South	0.93 ± 0.03	0.65 ± 0.04	<i>Rhododendron pingianum</i> Fan; <i>Abies georgei</i> var. <i>smithii</i>
4333	94.7071	29.6346	28	South	0.71 ± 0.03	0.41 ± 0.02	<i>Rhododendron pingianum</i> Fan; <i>Abies georgei</i> var. <i>smithii</i>

Index measurements

The collected seedlings were divided into above- and underground parts, and the plant height, aboveground diameter, horizontal root length (HRL), and vertical root length (VRL) of underground parts were measured. When measuring underground parts, the root system was gently shaken to dislodge the soil adhered to the roots. The remaining soil attached to the root surface was flushed with distilled water to maintain the natural growth condition of the root system. The roots were then spread on clean filter paper to absorb the excess water. A Vernier caliper was used to measure HRL and VRL. Here, HRL was defined as the horizontal spread of roots and VRL was defined as the vertical extension of roots. After HRL and VRL were measured, the root samples were scanned by the WinRHIZO Root Analysis System (WinRHIZO TRON 2009, Regent Instruments Inc., Canada) to analyze the average length and diameter of fine roots and other indicators. After scanning, fine roots were separated from taproots according to the criteria fine roots: diameter < 2 mm and thick roots: diameter \geq 2 mm (Qi et al., 2020). The separated fine roots were placed in an envelope, dried in the oven at 80 °C to a constant weight, and then weighed (dry weight, g). The characteristics of seedlings of different age groups are shown in *Table 2*.

The physical and chemical properties of the soil samples were determined after air drying. After removing stones and visible plant roots, the soil samples were passed through a 0.25 mm screen. Soil water content (SWC) was measured by the 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 Fang et al. (2014).

Statistical analysis

The normality of the variances was tested using raw data via the Kolmogorov–Smirnov test ($p = 0.05$), and the homogeneity of these variances was tested using Levene’s test ($p > 0.05$). These calculations were conducted using SPSS 26.0 (IBM, USA). One-way ANOVA and Tukey’s HSD test were used to determine differences in statistical parameters (e.g., root distribution parameters and soil physical and chemical properties) across the root distributions and FRBs of seedlings at different elevations and ages ($p \leq 0.05$). In addition, we used two-factor ANOVA to analyze the effects of elevation, stand age and elevation \times stand age on seedling root indexes. Statistical analyses (i.e., mean \pm standard deviation) were conducted using Excel 2013 (Microsoft, USA) and SPSS 26.0. ((IBM Corp., Armonk, NY, United States)). All charts depicting

variations in parameters were generated using Origin 2021 (OriginLab, Northampton, MA, USA). Redundancy analysis (RDA) was performed using Canoco 5.0 (Microcomputer Power, USA) to evaluate the effects of environmental factors on the root distributions and FRBs of different seedling age groups. Prior to RDA, the significance of the effect of each variable was assessed using a Monte Carlo permutation test.

Table 2. Characteristics of *Abies georgei* var. *smithii* seedlings of different age levels

Elevation (m)	Age groups	Average plant height (cm)	Mean ground diameter (mm)	Mean diameter of fine roots (mm)	Mean length of fine roots (cm)
3837	1-2	4.17 ± 1.33 Ba	0.57 ± 0.16 Ba	0.27 ± 0.09 Ba	0.46 ± 0.3 Ca
	3-4	4.53 ± 1.45 Bcd	0.64 ± 0.08 Bb	0.27 ± 0.02 Bbc	0.78 ± 0.09 Cbc
	5-6	10.87 ± 2.32 Aa	2.65 ± 0.73 Aa	0.67 ± 0.07 Aa	3.07 ± 1.39 Ba
	7-8	11.93 ± 3.7 Aa	2.53 ± 1.1 Aa	0.73 ± 0.12 Aa	3.44 ± 0.83 Bab
	9-10	16.53 ± 2.9 Aa	4.15 ± 0.79 Aa	0.84 ± 0.16 Aab	5.89 ± 0.45 Aa
3953	1-2	3.83 ± 0.49 Ca	0.63 ± 0.11 Ca	0.2 ± 0.13 Ba	0.31 ± 0.2 A a
	3-4	8.9 ± 1.75 ABCab	1.56 ± 0.56 BCa	0.42 ± 0.03 Aa	2.19 ± 0.92 Aa
	5-6	7.33 ± 1.92 BCa	2.21 ± 0.39 BCa	0.44 ± 0.04 Ab	1.19 ± 0.75 Aa
	7-8	11.2 ± 2.5 ABa	2.88 ± 0.52 ABa	0.43 ± 0.09 Aab	1.17 ± 0.19 Ab
	9-10	14.63 ± 3.67 Aa	4.54 ± 1.6 Aa	0.53 ± 0.04 Ab	5.18 ± 4.57 Aa
4021	1-2	2.12 ± 0.32 Ca	0.56 ± 0.03 Ba	0.2 ± 0.06 Da	0.44 ± 0.43 Ba
	3-4	3.86 ± 0.55 BCd	0.66 ± 0.11 Bb	0.22 ± 0.04 CDc	0.32 ± 0.16 Bc
	5-6	10.1 ± 2.1 ABCa	1.79 ± 0.96 Ba	0.37 ± 0.04 BCb	1.98 ± 0.76 ABa
	7-8	10.93 ± 1.94 ABa	3.07 ± 0.58 ABa	0.44 ± 0.1 ABab	2.74 ± 1.3 ABab
	9-10	17.97 ± 6.52 Aa	4.61 ± 1.9 Aa	0.57 ± 0.04 Aab	4.8 ± 2.23 Aa
4111	1-2	4.1 ± 0.78 Ca	0.79 ± 0.03 Ca	0.18 ± 0.06 Ba	0.49 ± 0.08 Ba
	3-4	10.4 ± 0.56 AaB	1.87 ± 0.23 BCa	0.35 ± 0.07 ABab	1.85 ± 0.13ABab
	5-6	8.93 ± 0.81 Ba	2.35 ± 0.19 BCa	0.33 ± 0.05 ABb	1.91 ± 1.11 ABa
	7-8	10.6 ± 1.93 ABa	3.2 ± 0.77 Ba	0.33 ± 0.06 ABb	2 ± 1.04 ABab
	9-10	14.47 ± 2.5 Aa	5.54 ± 1.01 Aa	0.5 ± 0.08 Ab	3.18 ± 1.19 Aa
4206	1-2	3.73 ± 0.72 Ca	0.65 ± 0.13 Da	0.23 ± 0.02ABCa	0.32 ± 0.1 Cabc
	3-4	7 ± 0.53 BCbc	1.54 ± 0.27 CDa	0.22 ± 0.04 BCc	1.53 ± 0.17 BCa
	5-6	10.13 ± 0.81 BCa	2.15 ± 0.63Ca	0.16 ± 0.04 Cc	1.78 ± 1.15 BCa
	7-8	11.7 ± 3.91 ABa	3.19 ± 0.14Ba	0.51 ± 0.24 ABab	4.49 ± 1.2 Aa
	9-10	18.8 ± 5.11 Aa	4.73 ± 0.26Aa	0.53 ± 0.07 Ab	2.74 ± 0.42 ABa
4333	1-2	4.2 ± 1.22 Ca	0.89 ± 0.36Ca	0.38 ± 0.03 Ba	0.62 ± 0.61 Aa
	3-4	9.4 ± 1.01 Bab	1.72 ± 0.32Ca	0.42 ± 0.04 Ba	1.25 ± 0.76Aabc
	5-6	9.27 ± 1.25 Ba	1.75 ± 0.38Ca	0.33 ± 0.07 Bb	2.32 ± 0.87 Aa
	7-8	13.17 ± 3.52 ABa	3.67 ± 0.3Ba	0.63 ± 0.04 ABab	3.08 ± 1.69 Aab
	9-10	15.1 ± 0.78 Aa	4.74 ± 0.52Aa	1.07 ± 0.41 Aa	6.32 ± 5.04 Aa

Different capital letters indicate significant differences among seedlings of different age groups at the same elevation ($p < 0.05$). Different lowercase letters indicate significant differences among seedlings of the same age group at different elevations ($p < 0.05$)

Results

Distribution characteristics of the horizontal and vertical root lengths of seedlings as a function of elevation

The average HRL of the five age grades of seedlings ranged from 0.83 ± 0.53 cm to 15.90 ± 7.19 cm (Table A2), but no significant difference in HRL was observed at all seedling age levels ($p > 0.05$) except at 3–4 years (Fig. 2; Table A2). The average VRL of the seedlings ranged from 2.66 ± 1.29 cm to 13.55 ± 4.99 cm (Table A2), and no significant difference among elevation bands was noted ($p > 0.05$; Fig. 2; Table A2). The HRL of seedlings growing at the same elevation significantly differed among the different age groups ($p < 0.05$). However, no significant difference in VRL between different age groups was observed at 4300 m ($p > 0.05$). Significant differences in VRL among different age groups were observed at the five other elevations ($p < 0.05$).

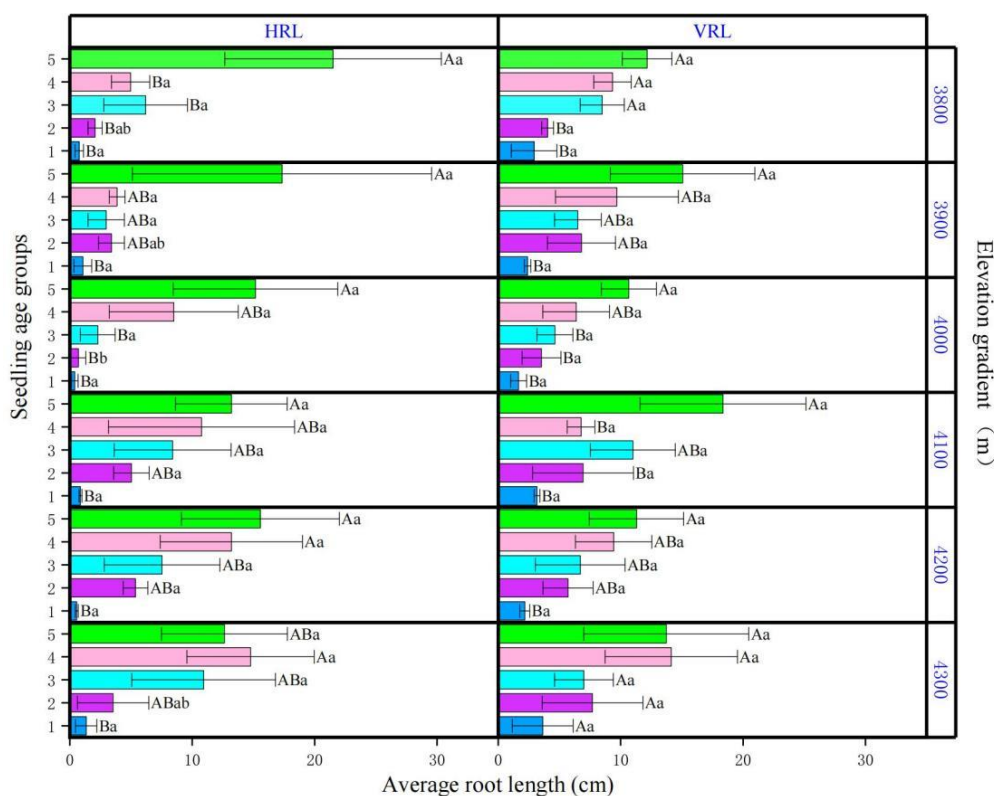


Figure 2. Root distribution characteristics of seedlings of different age levels as a function of elevation. Error bars represent one SD (std. deviation). HRL: Horizontal root length; VRL: Vertical root length. 1: 1–2-year-old seedlings; 2: 3–4-year-old seedlings; 3: 5–6-year-old seedlings; 4: 7–8-year-old seedlings; 5: 9–10-year-old seedlings. Different capital letters indicate significant differences among seedlings of different age groups at the same elevation ($p < 0.05$). Different lowercase letters indicate significant differences among seedlings of the same age level at different elevations ($p < 0.05$)

Distribution characteristics of the fine root biomass of seedlings of different age levels as a function elevation

The FRB of seedlings of different age levels ranged from 0.01 ± 0.01 g to 0.90 ± 0.53 g (Table A2). The FRB of 9–10-year-old seedlings at 4100 m was larger

than the FRBs of all other seedling age levels. The FRB of the first four age grades (1–2 years, 3–4 years, 5–6 years, and 7–8 years) decreased with the elevation. Except for 3–4- and 5–6-year-old seedlings, no significant difference in FRB was observed among other age levels (1–2 years, 7–8 years, 9–10 years) as a function at the same elevation ($p > 0.05$) (Fig. 3; Table A2). At the same elevation, the FRB of 9–10-year-old seedlings was significantly higher than that of the four other age grades ($p < 0.05$).

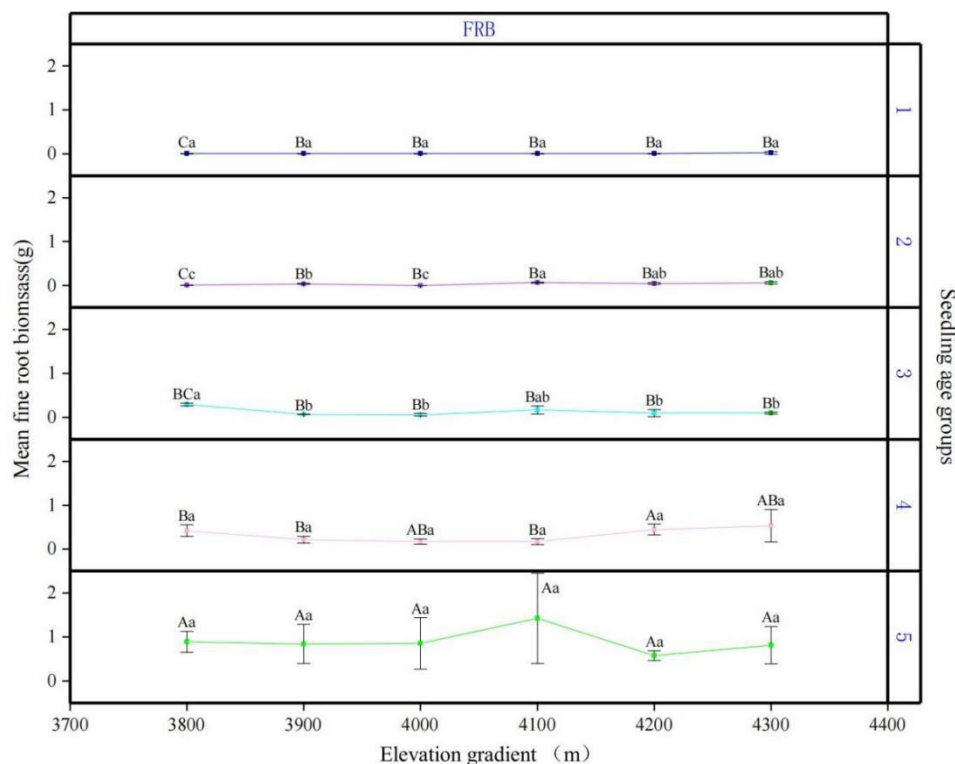


Figure 3. Fine root biomass of seedlings of different age levels as function of elevation. Error bars represent one SD (std. deviation). FRB: Fine root biomass. 1: 1–2-year-old seedlings; 2: 3–4-year-old seedlings; 3: 5–6-year-old seedlings; 4: 7–8-year-old seedlings; 5: 9–10-year-old seedlings. Different capital letters indicate significant differences among seedlings of different age groups at the same elevation ($p < 0.05$). Different lowercase letters indicate significant differences among seedlings of the same age level at different elevations ($p < 0.05$)

Effects of elevation and age level on the root length growth and FRB of *Abies georgei* var. *smithii* seedlings

HRLs decreased in the order of 4300 m > 4200 m > 4100 m > 3800 m > 3900 m > 4000 m; VRLs decreased in the order of 4100 m > 4300 m > 3900 m > 3800 m > 4200 m > 4000 m; and FRB decreased in the order of 4100 m > 3800 m > 4300 m > 3900 m > 4200 m > 4000 m. The HRL, VRL and FRB of *A. georgei* var. *smithii* seedlings were lowest at 4000 m and increased with increasing age level (Table A2). The results of two-factor ANOVA showed (Table 3) that elevation had no significant effect on HRL, VRL and FRB of *Abies georgei* var. *Smithii* seedlings ($p > 0.05$), while age groups had extremely significant effect on them ($p < 0.001$). The combined effect of elevation and age groups also showed no significant effect ($p > 0.05$). Regression analysis was conducted on the relationship

between stand age and seedling root indexes (Table 3). The results showed that HRL, VRL and FRB at different elevations showed a binomial growth trend with the increase of forest age, and the regression equation had a high fitting degree. At different elevations, HRL, VRL and FRB were significantly correlated with stand age ($p < 0.05$).

Table 3. Analysis of variance of HD, VD, FRB were performed on the *Abies Georgei* var. *smithii* seedlings, and linear regression analysis of root index and stand age of seedlings at different elevations

ANOVA	HRL			VRL			FRB		
EL	0.551ns			1.344ns			0.297ns		
AL	27.443***			25.031***			36.159***		
EL x AL	1.252ns			0.905ns			1.049ns		
Residuals	22.021			10.814			0.06789		
Elevation/m	Regression equation	R ²	p-value	Regression equation	R ²	p-value	Regression equation	R ²	p-value
3837	$y = 4.43x - 6.21$	0.546	$P < 0.001$	$y = 2.37x + 0.26$	0.819	$p < 0.001$	$y = 0.219x - 0.334$	0.822	$p < 0.001$
3953	$y = 3.30x - 4.17$	0.348	$P < 0.05$	$y = 2.82x - 0.37$	0.556	$p < 0.001$	$y = 0.185x - 0.324$	0.552	$p < 0.01$
4021	$y = 3.73x - 5.79$	0.630	$p < 0.001$	$y = 2.08x - 0.87$	0.723	$p < 0.001$	$y = 0.188x - 0.345$	0.468	$p < 0.01$
4111	$y = 3.04x - 1.46$	0.533	$p < 0.01$	$y = 3.02x + 0.17$	0.453	$p < 0.01$	$y = 0.295x - 0.520$	0.409	$p < 0.05$
4206	$y = 3.78x - 2.90$	0.652	$p < 0.001$	$y = 2.20x + 0.46$	0.593	$p < 0.001$	$y = 0.154x - 0.229$	0.819	$p < 0.001$
4333	$y = 3.38x - 1.51$	0.530	$p < 0.01$	$y = 2.66x + 1.25$	0.425	$p < 0.01$	$y = 0.205x - 0.312$	0.601	$p < 0.001$

HRL: horizontal root length; VRL: vertical root length; FRB: fine root biomass; EL: elevation; AL: age level
*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns: no significance

Effects of soil properties on the root growth and FRB of *Abies georgei* var. *smithii* seedlings

According to the results of the Monte Carlo permutation test, all soil factors (i.e., AP, AK, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, TP, TK, TN, TOC, SWC, ST, EOC, DOC, POC) explained 83.2% of the variation in root length of seedlings of all age levels (HRL1, HRL2, HRL3, HRL4, HRL5, VRL1, VRL2, VRL3, VRL4, VRL4, and VRL5). The cumulative percentage of species–environment relationships between axes 1 and 2 was 65.14%, and Axis 1 accounted for 40.27% of the interpretation ratio, which means seedling root growth and soil factors are highly correlated and could well reflect the influence of dominant factors on seedling root growth (Fig. 4A). Among the 13 soil factors, $\text{NH}_4^+\text{-N}$ and POC had the largest contribution value and significant influence on the root growth of seedlings ($P < 0.05$), indicating that $\text{NH}_4^+\text{-N}$ and POC were the main soil factors affecting the root growth of seedlings (Table 4).

According to the results of the Monte Carlo permutation test, all soil factors (i.e., AP, AK, $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, TP, TK, TN, TOC, SWC, ST, EOC, DOC, POC) explained 72.7% of the variation in FRB (FRB1, FRB2, FRB3, FRB4, and FRB5) of seedlings of all levels. The cumulative percentage of species–environment relationships between axes 1 and 2 was 97.43%, and Axis 1 accounted for 86.48% of the interpretation ratio, which indicates that FRB is highly correlated with soil factors and could well reflect the influence of leading factors on seedling root growth (Fig. 4B). Among the 13 soil factors studied, AP contributed the most to FRB ($p < 0.05$), which indicates that AP is the main soil factor affecting the FRB of *A. georgei* var. *smithii* seedlings (Table 4).

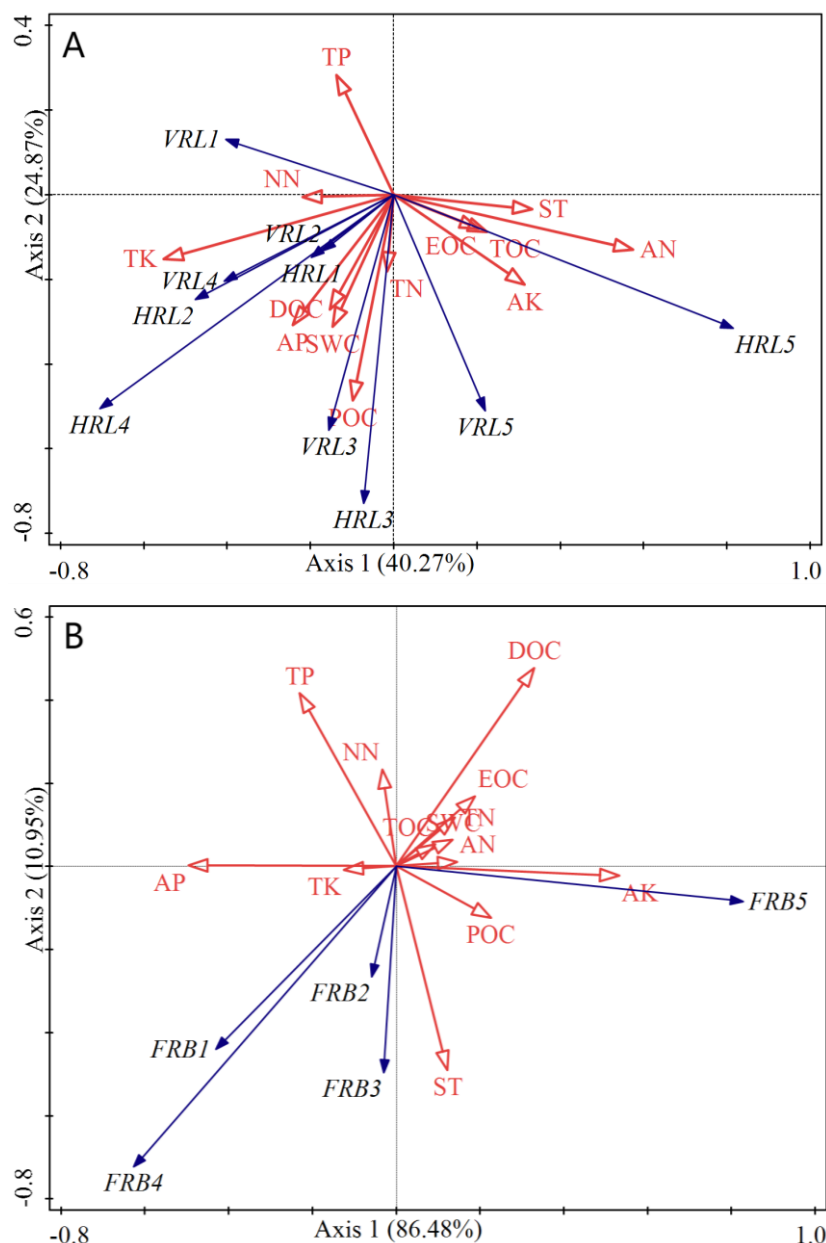


Figure 4. Relationships between soil properties and root distributions. (A) RDA double sequence diagrams of HRL, VRL and soil factors at different ages; (B) RDA double sequence diagrams of FRB and soil factors at different ages. Red arrows: root indexes; Blue arrows: soil factors. HRL: Horizontal root length; VRL: Vertical root length; FRB: Fine root biomass. AN: $\text{NH}_4^+\text{-N}$; NN: $\text{NO}_3^-\text{-N}$. 1: 1–2-year-old seedlings; 2: 3–4-year-old seedlings; 3: 5–6-year-old seedlings; 4: 7–8-year-old seedlings; 5: 9–10-year-old seedlings. ST: Soil temperature; SWC: Soil water content; TOC: Total organic carbon; TN: Total nitrogen; TP: Total phosphorus; TK: Total potassium; AK: available potassium; AP: Available phosphorus; $\text{NO}_3^-\text{-N}$: Nitrate nitrogen; $\text{NH}_4^+\text{-N}$: Ammonium nitrogen; POC: Particulate organic carbon; EOC: Easily oxidized organic carbon; DOC: Dissolved organic carbon

The results of RDA (Tables A3, A4, and A5) showed that 13 soil factors have different effects on the HRL, VRL and FRB of *A. georgei* var. *smithii* seedlings at different age levels. The main soil factors affecting HRL were ST and AK (1–2 years);

NO₃⁻-N (3–4 years); AP (5–6 years); TK and NO₃⁻-N (7–8 years); and NH₄⁺-N and SWC (9–10 years). The main soil factors affecting the VRL of *A. georgei* var. *smithii* seedlings were NH₄⁺-N (1–2 years); NO₃⁻-N, TK, and TP (3–4 years); TP (5–6 years); DOC (7–8 years); and ST and DOC (9–10 years). The main soil factors affecting FRB were TK, SWC, and NO₃⁻-N (1–2 years); TK (3–4 years); ST (5–6 years); TK and DOC (7–8 years); and AP (9–10 years). Figure 4 clearly shows the correlation between soil factors and root growth, FRB of seedlings of different age groups. As can be seen from Figure 4A, VRL1 were located in the upper left corner of the RDA plot and positively correlated with NO₃⁻-N (NN) and TP but negatively correlated with NH₄⁺-N (AN) and AK. HRL1, HRL2, HRL3, HRL4, VRL2, VRL3 and VRL4 were located at the left end of RDA axis 1 and positively correlated with TK, SWC, POC, and AC. HRL5 and VRL5 were located at the lower right corner of the sequence diagram. NH₄⁺-N (AN), AK, and TOC were positively correlated with HRL5 and VRL5, but negatively correlated with TP. Figure 4B shows that FRB1, FRB2, FRB3 and FRB4 are located at the left end of RDA axis 1, and are positively correlated with TK, AP and ST, but negatively correlated with DOC, TP and AK. FRB5 is located at the lower right corner of the sorting diagram, and is positively correlated with AK and POC, while negatively correlated with TK and AP.

Table 4. Contribution rates and *P* values of soil factors to the RD and FRB of *Abies georgei* var. *smithii* seedlings

RD			FRB		
Name	Contribution %	<i>p</i> -value	Name	Contribution %	<i>p</i> -value
POC	15	0.022	AP	28.5	0.034
NH ₄ ⁺ -N	15	0.046	DOC	15	0.074
DOC	8	0.244	AK	24.7	0.086
ST	9.6	0.122	ST	5.3	0.334
TK	8.8	0.124	NO ₃ ⁻ -N	4.6	0.362
TP	6.8	0.262	TK	4.7	0.372
SWC	7.3	0.21	NH ₄ ⁺ -N	1.2	0.73
AP	6.2	0.286	TN	3.8	0.462
EOC	3.2	0.706	SWC	2.4	0.606
TOC	6.5	0.3	POC	2.8	0.572
NO ₃ ⁻ -N	3.6	0.64	TP	1.7	0.73
AK	6.9	0.24	TOC	2.8	0.636
TN	3.4	0.594	EOC	2.5	0.672

RD: Root distribution; FRB: Fine root biomass; ST: Soil temperature; SWC: Soil water content; TOC: Total organic carbon; TN: Total nitrogen; TP: Total phosphorus; TK: Total potassium; AK: available potassium; AP: Available phosphorus; NO₃⁻-N: Nitrate nitrogen; NH₄⁺-N: Ammonium nitrogen; POC: Particulate organic carbon; EOC: Easily oxidized organic carbon; DOC: Dissolved organic carbon

Discussion

Distribution characteristics of the root growth and fine root biomass of Abies georgei var. *smithii* seedlings as a function of elevation

Plant growth and development are largely affected by the environment, and harsh environments tend to inhibit the development of plant organs (Bryndís, 2017; Du et al.,

2012; Guadalupe et al., 2013). In the seedling stage, plants obtain water and nutrients from the soil layer through the horizontal and vertical extension of roots (Grill and Hubertl, 1998; Mulumba and Lal, 2008). Our results showed that the vertical roots of *A. georgei* var. *smithii* seedlings are mainly distributed in the 0–20 cm soil layer; moreover, the roots of the species extend horizontally over a distance of 0–25 cm. Both HRL and VRL increased with increasing seedling age level (Fig. 2), and significant differences were observed among different age classes ($p < 0.001$) (Table 3). These findings are consistent with a previous study involving Norwegian forests, which found that tree age has a significant effect on spruce root distribution ($p < 0.05$; Isabella et al., 2008). Some researchers have also found that the root length of *Quercus wutaishansea* seedlings in the Loess Plateau region of China increases from 3.34 ± 0.56 cm to 5.15 ± 0.67 cm with increasing age grade (Xia et al., 2012).

In previous studies, physiological characteristics of seedlings at different elevation bands were different (Reinhardt et al., 2011), and elevation has been shown to influence plant growth strongly (Takahashi, 2010; Pickering and Green, 2009). This parameter mainly controls plant traits and ecosystem functions by indirectly changing other driving factors, such as soil properties and species diversity (Fu et al., 2020; Case et al., 2005). In this study, we found no significant difference between the HRL and VRL of seedlings of different age levels along the elevation bands ($p > 0.05$) (Table 3), which contradicts the results of previous research (Marcora et al., 2016). Thus, our hypothesis (1) is rejected. This finding may be explained by that fact that, as the dominant population in Sejila Mountain, *A. georgei* var. *smithii* is well adapted to the climate of high elevation areas; thus, the physiological characteristics of its seedlings are minimally affected by elevations in the range of 3800–4100 m. Only when the elevation exceeds 4400 m do the physiological indices of the species change drastically under the influence of elevation (Liu et al., 2017). In this study, because only seedlings grown in the elevation range of 3800–4300 m were collected, minimal differences in root distribution were observed along the elevation bands.

Studying the distribution of underground root biomass is more challenging than studying the aboveground biomass of plants because the former requires more work and resources (Vogt et al., 1995; Hu et al., 2005; Hendricks et al., 2006; Metcalfe et al., 2007). Studies have shown that FRB increases with increasing forest age (Makkonen and Helmisaari, 2001). FRB and biomass-related morphological characteristics follow the same trend as the time series (Isabella et al., 2008). Our study confirmed that FRB significantly differs among different age grades ($p < 0.001$) (Table 3) and gradually increases with increasing age of *A. georgei* var. *smithii* seedlings (Fig. 3). We further studied the effect of elevation on FRB and found no difference in seedling FRB among different elevation bands ($p > 0.05$) (Table 3). Studies have demonstrated that the FRB of spruce forests in Northern Europe, Central Europe, and the European Alps increases significantly with elevation and that the greatest FRB is nearly twice that of the lowest stand (Hertel and Schling, 2011). In the Peruvian Andes, Girardin et al. findings fine root biomass gradually increased along the elevation bands (194–3020 m) and reached the maximum at 2020 m (Girardin et al., 2010). In the Changbai Mountain Nature Reserve, China, the FRB decreases significantly with elevation (Zhou et al., 2013), which is inconsistent with the results of our research. Such a finding indicates that elevation is not the main factor affecting the root growth of *A. georgei* var. *smithii* seedlings in high-elevation areas (Liu et al., 2017). This is consistent with Ji et al. findings that fine root biomass is not affected by elevation in southwest China (Ji et al., 2019).

However, other studies on the FRB of adult *A. georgei* var. *smithii* in Sejila Mountain found high FRBs at 3900 m and 4200 m; specifically, the FRB is highest at 3900 m (Xin et al., 2017), and significant differences in FRB between these elevations could be observed ($p < 0.01$). These results indicate that the roots of *A. georgei* var. *smithii* in the alpine regions of Southeast Asia do not yet show differentiation characteristics with elevation at the seedling stage.

Effects of soil factors on the root growth and FRB of Abies georgei var. smithii seedlings

Studies have found that environmental heterogeneity, such as that due to temperature, water, light, and soil, caused by elevation lead to changes in the root distribution and physiological and ecological characteristics of alpine plants (Pan et al., 2009). For example, it has been found that soil temperature may be responsible for limiting the growth performance of high-elevation conifer seedlings in British Columbia (Balisky and Burton, 1997). Of course, studies in different regions will have different results. In our study area, our results reveal that the environmental response of roots of *A. georgei* var. *smithii* seedlings from Sejila Mountain in Tibet is mainly reflected in the influence of soil factors and that the heterogeneity of soil properties is indirectly caused by changes among the elevation bands (Soethe et al., 2006). We found that $\text{NH}_4^+\text{-N}$ and POC greatly influence the root growth of *A. georgei* var. *smithii* seedlings ($p < 0.05$) (Table 4). A sufficient N supply could change the process of root growth and development, thereby increasing root weight and diameter (Mackiedaw Son et al., 1995). $\text{NH}_4^+\text{-N}$ could directly affect the root length and root dry matter accumulation of seedlings (Viciedo and Dilier, 2017). SOC is a key factor affecting plant root growth and development (Vogel et al., 2005; Ruess et al., 2003; Dam et al., 1997), while POC, a component of persistent soil active organic carbon, is involved in the growth and development of various plant components (Witzgall et al., 2021).

Establishing the relationship between root biomass and its limiting factors is especially important in alpine ecosystems because the distribution and degradation of permafrost and uncertain environmental factors may affect FRB (Chang et al., 2012; Li et al., 2011). Studies have shown that soil factors strongly affect FRB, yield, and turnover in boreal forests (Pechackova et al., 1999; Yuan and Chen, 2010). The present study found that AP is the major contributor to FRB at different seedling age levels, consistent with the previous finding that AP affects the FRB in northern Queensland rainforests (Maycock and Congdon, 2000). In addition, studies have found that nutrient turnover in fine roots decreases with elevation at high elevation (Garkoti, 2012), but subalpine *A. georgei* var. *Smithii* have a unique nutrient acquisition strategy, with greater input of biomass and more active metabolism as the reason for *A. georgei* var. *Smithii* to absorb more soil nutrients (Ugawa et al., 2010). It is not difficult to understand that the fine root biomass of *A. georgei* var. *Smithii* seedlings is less affected by elevation. Therefore, soil factors, rather than elevation, are the most important factors affecting the growth of *A. georgei* var. *Smithii* seedlings.

Conclusions

The root growth and FRB of *A. georgei* var. *smithii* seedlings increased with their age level. While no difference in the characteristics of *A. georgei* var. *smithii* roots as a function of elevation were observed at the seedling stage, changes in soil properties

caused by the elevation significantly affected the root growth and FRB of the seedlings. Our results revealed variations in the root growth and FRB of *A. georgei* var. *smithii* seedlings as a function of elevation and age level, as well as their correlation with soil factors. Our findings enrich the knowledge on underground ecosystems of natural forests in high-elevation areas and provide data support for the regeneration and conservation of dominant species in subalpine forest ecosystems. However, this study presents some limitations because we did not evaluate elemental differences between seedling roots of different age levels (Cao et al., 2020) or fully explore environmental factors, such as soil microbial diversity, at different elevations in the study area. Therefore, we encourage future researchers to explore, in detail, the effects of environmental factors on the chemical elements of seedling roots and exert efforts to reveal the complete growth characteristics and influencing mechanisms of *A. georgei* var. *smithii* seedlings in southeast Tibet.

Acknowledgments. This work was supported by the National Natural Science Foundation of China (31960256), Graduate Innovation Program of Key Laboratory of Forest Ecology in Tibet Plateau, Ministry of Education (XZA-JYBSYS-2021-Y13) and the Independent Research Project of Science and Technology Innovation Base in Tibet Autonomous Region (XZ2022JR0007G).

REFERENCES

- [1] Balisky, A. C., Burton, P. (1997): Planted conifer seedling growth under two soil thermal regimes in high-elevation forest openings in interior British Columbia. – *New Forests* 14(1): 63-82. DOI: 10.1023/A:1006592705104.
- [2] Bardgett, R. D., Mommer, L., De Vries, F. T. (2014): Going underground: root traits as drivers of ecosystem processes. – *Trends Ecol. Evol.* 29(12): 692-699. DOI: 10.1016/j.tree.2014.10.006.
- [3] Bristiel, P., Roumet, C., Violle, C., Volaire, F. (2019): Coping with drought: root trait variability within the perennial grass *Dactylis glomerata* captures a trade-off between dehydration avoidance and dehydration tolerance. – *Plant Soil* 434: 327-342. DOI: 10.1007/s11104-018-3854-8.
- [4] Bryndís, M. (2014): Seed rain and seed bank reveal that seed limitation strongly influences plant community assembly in grasslands. – *PLoS ONE* 9(7): 1-7. DOI: 10.1371/journal.pone.0103352.
- [5] Cao, Y., Li, Y., Zhang, G., Zhang, J., Chen, M. (2020): Fine root C:N:P stoichiometry and its driving factors across forest ecosystems in northwestern China. – *Science of the Total Environment* 737: 140299. DOI: 10.1016/j.scitotenv.2020.140299.
- [6] Case, M. J., Peterson, D. L. (2005): Fine-scale variability in growth-climate relationships of Douglas-fir, north cascade range, Washington. – *Can. J. For. Res.* 35: 2743-2755. DOI: 10.1139/x05-191.
- [7] Chang, R., Fu, B., Liu, G., Yao, X., Shuai, W. (2012): Effects of soil physicochemical properties and stand age on fine root biomass and vertical distribution of plantation forests in the loess plateau of China. – *Ecological Research* 27(4): 827-836. DOI: 10.1007/s11284-012-0958-0.
- [8] Chen, X., Yang, Q., Chen, Z., Xuexiao, Y. U., Yang, Q., Lei, J. (2017): Distribution of soil easily oxidized organic carbon and its response to soil factors in the tropical coastal forest of Hainan Island, China. – *Journal of Central South University of Forestry & Technology* 37(11): 140-145 (in Chinese).

- [9] Dam, D. V., Breemen, N. V., Veldkamp, E. (1997): Soil organic carbon dynamics: variability with depth in forested and deforested soils under pasture in costa rica. – *Biogeochemistry* 39(3): 343-375. DOI: 10.1023/A:1005880031579.
- [10] Deng, L., Guan, J. H., Zhang, W. H. (2018): Response of root morphological characteristics of *Quercus liaotungensis* seedlings to environmental gradients. – *Acta Ecologica Sinica* 38(16): 5739-5749 (in Chinese).
- [11] Dorich, R. A., Nelson, D. W. (1983): Direct colorimetric measurement of ammonium in potassium chloride extracts of soils. – *Soil Science Society of America Journal* 47(4): 833-836. DOI: 10.2136/sssaj1983.03615995004700040042x.
- [12] Du, Y. J., Mi, X. C., Liu, X. J., Ma, K. (2012): The effects of ice storm on seed rain and seed limitation in an evergreen broad-leaved forest in east China. – *Acta Oecologica* 39: 87-93. DOI: 10.1016/j.actao.2012.01.006.
- [13] Duan, F., Fang, J. P., Zhou, C. N. (2020): Study on the relationship between the release characteristics of organic carbon from litters and soil organic carbon pool in Tibetan primitive dark coniferous forest. – *Journal of Soil and Water Conservation* 34(03): 349-355 (in Chinese).
- [14] Dunne, J. A., Saleska, S. R., Fischer, M. L., Harte, J. (2004): Integrating experimental and gradient methods in ecological climate change research. – *Ecology* 85: 904-916. DOI: 10.1890/03-8003.
- [15] Eissenstat, D. M. (1992): Costs and benefits of constructing roots of small diameter. – *J. Plant Nutr* 15(6-7): 763-782. DOI: 10.1080/01904169209364361.
- [16] Fang, H. J., Cheng, S. L., Yu, G. R., Xu, M. J., Wang, Y. S. (2014): Experimental nitrogen deposition alters the quantity and quality of soil dissolved organic carbon in an alpine meadow on the Qinghai-Tibetan plateau. – *Applied Soil Ecology* 81: 1-11. DOI: 10.1016/j.apsoil.2014.04.007.
- [17] Ferguson, S. D., Leger, E. A., Li, J., Nowak, R. S. (2015): Natural selection favors root investment in native grasses during restoration of invaded fields. – *J Arid Environ* 116: 11-17. DOI: 10.1016/j.jaridenv.2015.01.009.
- [18] Foster, A. C., Martin, P. H., Redmond, M. D. (2020): Soil moisture strongly limits Douglas-fir seedling establishment near its upper elevational limit in the southern Rocky Mountains. – *Canadian Journal of Forest Research* 50: 1-22. DOI: 10.1139/cjfr-2019-0296.
- [19] Fu, H., Yuan, G., Ge, D., Li, W., Jeppesen, E. (2020): Cascading effects of elevation, soil moisture and soil nutrients on plant traits and ecosystem multi-functioning in Poyang Lake wetland, China. – *Aquatic Sciences* 82(34): 1-10. DOI: 10.1007/s00027-020-0711-7.
- [20] Gammon, N. (1951): Determination of total potassium and sodium in sandy soils by flame photometer. – *Soil Science* 71(3): 211-214. DOI: 10.1021/ac60051a025.
- [21] Garkoti, S. C. (2012): Dynamics of fine root N, P and K in high elevation forests of central Himalaya. – *Forestry Studies in China* 14: 1. DOI: 10.1007/s11632-012-0203-5.
- [22] Garten, C. T., Post, W. M., Hanson, P. J., Cooper, L. W. (1999): Forest soil carbon inventories and dynamics along an elevation gradient in the southern Appalachian Mountains. – *Biogeochemistry* 1999: 45(2): 115-145. DOI: 10.1023/A:1006121511680.
- [23] Girardin, C., Malhi, Y., Leoc Aragão, Mamani, M., Huasco, W. H., Durand, L., et al. (2010): Net primary productivity allocation and cycling of carbon along a tropical forest elevational transect in the Peruvian Andes. – *Global Change Biology* 16(12): 3176-3192. DOI: 10.1111/j.1365-2486.
- [24] Gonzalez-Ollauri, A., Hudek, C., Mickovski, S. B., Viglietti, D., Freppaz, M. (2021): Describing the vertical root distribution of alpine plants with simple climate, soil, and plant attributes. – *Catena* 203(1): 105305. DOI: 10.1016/j.catena.2021.105305.
- [25] Grill, E., Hubert, Z. (1998): A plant's dilemma. – *Science* 282: 252-253. DOI: 10.1126/science.282.5387.252.

- [26] Guadalupe, G., Pablo, O. B., Scopel, A. L., Hutchings, M. J. (2013): The dynamics of three shrub species in a fire-prone temperate savanna: the interplay between the seed bank, seed rain and fire regime. – *Plant Ecology* 214(1): 75-86. DOI: 10.1007/s11258-012-0147-9.
- [27] Haby, V. A. (1989): Soil no₃-n analysis in ca(oh)₂ extracts by the chromotropic acid method. – *Soil Science Society of America Journal* 53(1): 308-310. DOI: 10.2136/sssaj1989.03615995005300010059x.
- [28] Hanslin, H. M., Bischoff, A., Hovstad, K. A. (2019): Root growth plasticity to drought in seedlings of perennial grasses. – *Plant Soil* 440: 551-568. DOI: 10.1007/s11104-019-04117-7.
- [29] Harrison, S., LaForgia, M. (2019): Seedling traits predict drought-induced mortality linked to diversity loss. – *Proc Natl Acad Sci* 116: 5576-5581. DOI: 10.1073/pnas.1818543116.
- [30] Hendricks, J. J., Hendrick, R. L., Wilson, C. A., Mitchell, R. J., Pecot, S. D., Guo, D. (2006): Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. – *Journal of Ecology* 94(1): 40-57. DOI: 10.1111/j.1365-2745.2005.01067.x.
- [31] Hertel, D., Schling, D. (2011): Below-ground response of Norway spruce to climate conditions at Mt. Brocken (Germany)—a re-assessment of central Europe's northernmost treeline. – *Flora* 206(2): 127-135. DOI: 10.1016/j.flora.2010.05.001.
- [32] Hu, Z. M., Fan, J. W., Zhong, H. P., Han, B. (2005): Progress on grassland underground biomass researches in China. – *Chinese Journal of Ecology*. 124(9): 1095-1101 (in Chinese).
- [33] Isabella, B., De, W. H. A., Arne, S., Hooshang, M. (2008): Stand age and fine root biomass, distribution and morphology in a Norway spruce chronosequence in Southeast Norway. – *Tree Physiology* 28(5): 773-784. DOI: 10.1093/treephys/28.5.773.
- [34] Jackson, R., Manwaring, J., Caldwell, M. (1990): Rapid physiological adjustment of roots to localized soil enrichment. – *Nature* 344(6261): 58-60. DOI: 10.1038/344058a0.
- [35] Jakmune, J., Junsomboon, J. (2009): Determination of available phosphorus in soils by using a new extraction procedure and a flow injection amperometric system. – *Talanta* 79(4): 1076-1080. DOI: 10.1016/j.talanta.2009.01.028.
- [36] Ji, Z., Zhao, Y., Wang, Y. (2019): The trade-off between growth and reproduction in an alpine herbaceous plant along an elevation gradient. – *Pakistan Journal of Botany* 51(3): 1075-1080. DOI: 10.30848/PJB2019-3(41).
- [37] Jose, S. (2009): Agroforestry for ecosystem services and environmental benefits: an overview. – *Agroforestry Systems* 76(1): 1-10. DOI: 10.1007/s10457-009-9229-7.
- [38] Kato, T., Tang, Y., Song, G. U., Hirota, M., Zhao, X. (2006): Temperature and biomass influences on interannual changes in CO₂ exchange in an alpine meadow on the Qinghai-Tibetan Plateau. – *Global Change Biology* 12(7): 1285-1298. DOI: 10.1111/j.1365-2486.2006.01153.x.
- [39] King, J. S. (2021): Root biomass distribution and soil physical properties of short-rotation coppice American sycamore (*Platanus occidentalis* L.) grown at different planting densities. – *Forests* 12. DOI: 10.3390/f12121806.
- [40] Kramer-Walter, K. R., Bellingham, P. J., Millar, T. R., Smissen, R. D., Richardson, S. J., Laughlin, D. C. (2016): Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. – *J Ecol* 104: 1299-1310. DOI: 10.1111/1365-2745.12562.
- [41] Larson, J. E., Anacker, B. L., Wanous, S., Funk, J. L. (2020): Ecological strategies begin at germination: traits, plasticity and survival in the first 4 days of plant life. – *Funct Ecol* 34: 968-979. DOI: 10.1111/1365-2435.13543.
- [42] Leger, E. A., Atwater, D. Z., James, J. J. (2019): Seed and seedling traits have strong impacts on establishment of a perennial bunch-grass in invaded semi-arid systems. – *Journal of Applied Ecology* 97: 311-325. DOI: 10.1111/1365-2664.13367.

- [43] Leger, E. A., Goergen, E. M. (2017): Invasive *Bromus tectorum* alters natural selection in arid systems. – *J Ecol* 105: 1509-1520. DOI: 10.1111/1365-2745.12852.
- [44] Li, F., Xie, Y., Yang, G., Zhu, L., Hu, C., Chen, X., et al. (2016): Interactive influence of water level, sediment heterogeneity, and plant density on the growth performance and root characteristics of *Carex brevicuspis*. – *Limnologica* 62: 111-117. DOI: 10.1016/j.limno.2016.11.007.
- [45] Li, X., Minick, K. J., Luff, J., Noormets, A., King, J. S. (2019): Effects of microtopography on absorptive and transport fine root biomass, necromass, production, mortality and decomposition in a coastal freshwater forested wetland, southeastern USA. – *Ecosystems* 23: 1294-1308. DOI: 10.1007/s10021-019-00470-x.
- [46] Li, X., Zhang, X., Wu, J., Shen, Z., Wei, Y. (2011): Root biomass distribution in alpine ecosystems of the northern Tibetan Plateau. – *Environmental Earth Sciences* 64(7): 1911-1919. DOI: 10.1007/s12665-011-1004-1.
- [47] Liu, J. M., Xing, F. M., Yang, X. L., Zhao, K. T., Jia, L. M. (2017): Basic characteristics and physiological index changes of *Abies georgei* var. *smithii* seedlings at different altitudes of Shergyla Mountain. – *Journal of Zhejiang University (Agric. & Life Sci.)* 43(05): 623-630(in Chinese).
- [48] Lomolino, M. V. (2010): Elevation gradients of species-density: historical and prospective views. – *Glob Ecol Biogeogr* 10: 3-13. DOI: 10.1046/j.1466-822x.2001.00229.x.
- [49] Luo, D. (2010): Fruiting characteristics of *Abies georgei* var. *smithii* forest on the eastern slope of the Sejila Mountain in Tibet. – *Scientia Silvae Sinicae* 4398(1): 738901-18. DOI: DOI: 10.1117/12.835932.
- [50] Ma, W. H., Yang, Y. H., He, J. S., Zeng, H., Fang, J. Y. (2008): Above- and belowground biomass in relation to environmental factors in temperate grasslands, Inner Mongolia. – *Science in China Series C Life Sciences* 51(3): 263-279. DOI: 10.1007/s11427-008-0029-5.
- [51] Mackiedawson, L. A., Millard, Proe, M. F. (1995): The effect of nitrogen supply on root-growth and development in sycamore and Sitka spruce trees. – *Forestry* 68(2): 107-114. DOI: 10.1093/forestry/68.2.107.
- [52] Makkonen, H. S., Helmisaari. (2001): Fine root biomass and production in Scots pine stands in relation to stand age. – *Tree physiology* 21: 193-198. DOI: 10.1093/treephys/21.2-3.193.
- [53] Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P., Saatchi, S. (2010): Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. – *Global Change Biol* 16: 3171-3175. DOI: 10.1111/j.1365-2486.2010.02323.x.
- [54] Marcora, P. I., Tecco, P. A., Zeballos, S. R., Hensen, I. (2016): Influence of altitude on local adaptation in upland tree species from Central Argentina. – *Plant Biology* 19(2): 123-131. DOI: 10.1111/plb.12513.
- [55] Markesteijn, L., Poorter, L. (2009): Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. – *J Ecol* 97: 311-325. DOI: 10.1111/j.1365-2745.2008.01466.x.
- [56] Maycock, C. R., Congdon, R. A. (2000): Fine root biomass and soil N and P in north Queensland rain forests. – *Biotropica* 32(1): 185-190. DOI: 10.1111/j.1744-7429.2000.tb00460.x.
- [57] Metcalfe, D. B., Williams, M., Aragão, L. E. O. C., da Costa, A. C. L., de Almeida, S. S., Braga, A. P., et al. (2007): A method for extracting plant roots from soil which facilitates rapid sample processing without compromising measurement accuracy. – *New Phytol* 174(3): 697-703. DOI: 10.1111/j.1469-8137.2007.02032.x.
- [58] Mulumba, L. N., Lal, R. (2008): Mulching effects on selected soil physical properties. – *Soil & Tillage Research* 98(1): 106-111. DOI: 10.1016/j.still.2007.10.011.

- [59] Norby, R. J., Jackson, R. B. (2000): Root dynamics and global change: seeking an ecosystem perspective. – *New Phytol* 147: 3-12. DOI: 10.1046/j.1469-8137.2000.00676.x.
- [60] Paillex, A., Dolédec, S., Castella, E. (2013): Functional diversity in a large river floodplain: anticipating the response of native and alien macro-invertebrates to the restoration of hydrological connectivity. – *J Appl Ecol* 50: 97-106. DOI: 10.1111/1365-2664.12018.
- [61] Pan, H. L., Li, M. H., Cai, X. H., Wu, J., Du, Z., Liu, X. L. (2009): Responses of growth and ecophysiology of plants to altitude. – *Ecology and Environmental Sciences* 18(02): 722-730 (in Chinese).
- [62] Parent, S., Simard, M. J., Morin, H., Messier, C. (2003): Establishment and dynamics of the balsam fir seedling bank in old forests of northeastern Quebec. – *Canadian Journal of Forest Research* 33(4): 597-603. DOI: 10.1139/x02-194.
- [63] Pechackova, S., Doring, H. J., Rydlova, V., Herben, T. (1999): Species-specific spatial pattern of below-ground plant parts in a montane grassland community. – *Journal of Ecology* 87: 569-582. DOI: 10.1046/j.1365-2745.1999.00375.x.
- [64] Pickering, C. M., Green, K. (2009): Vascular plant distribution in relation to topography, soils and micro-climate at five glacia sites in the snowy mountains, Australia. – *Australian Journal of Botany* 57(3): 189-199. DOI: 10.1023/A:1014419309885.
- [65] Qi, Y. L. (2020): Influences of soil preparation measures on root distribution characteristics and ecological effect of plant communities on the loess plateau. – *Forestry College, Northwest A&F University* July, 2020. DOI: 10.27409/d.cnki.gxbnu.2020.001444.
- [66] Qi, Y., Wei, W., Chen, C., Chen, L. (2019): Plant root-shoot biomass allocation over diverse biomes: a global synthesis. – *Global Ecology and Conservation* 18: e00606. DOI: 10.1016/j.gecco.2019.e00606.
- [67] Qi, Y., Wei, W., Li, J., Chen, C., Huang, Y. (2020): Effects of terracing on root distribution of *Pinus tabulaeformis* carr. forest and soil properties in the Loess Plateau of China. – *Science of the Total Environment* 721: 137506. DOI: 10.1016/j.scitotenv.2020.137506.
- [68] Rahbek, C. (2005): The role of spatial scale and the perception of large-scale species-richness patterns. – *Ecol Lett* 8: 224-239. DOI: 10.1111/j.1461-0248.2004.00701.x.
- [69] Ramachandran Nair, P., Mohan Kumar, B., Nair, V. D. (2009): Agroforestry as a strategy for carbon sequestration. – *Journal of Plant Nutrition and Soil Science* 172(1): 10-23. DOI: 10.1002/jpln.200800030.
- [70] Reinhardt, K., Castanha, C., Germino, M. J., Kueppers, L. M. (2011): Ecophysiological variation in two provenances of *Pinus flexilis* seedlings across an elevation gradient from forest to alpine. – *Tree Physiology* 31(6): 615-625. DOI: 10.1093/treephys/tpr055.
- [71] Ronald, L., Hendrick, P. (1993): The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. – *Canadian Journal of Forest Research* 23(12): 2507-2520. DOI: 10.1021/ja00817a061.
- [72] Ruess, R. W., Hendrick, R. L., Burton, A. J., Pregitzer, K. S., Maurer, G. E. (2003): Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. – *Ecological Monographs* 73(4): 643-662. DOI: 10.1890/02-4032.
- [73] Schenk, H. J., Jackson, R. B. (2005): Mapping the global distribution of deep roots in relation to climate and soil characteristics. – *Geoderma* 126(1-2): 129-140. DOI: 10.1016/j.geoderma.2004.11.018.
- [74] Simpson, C. R., Gonzales, J., Enciso, J., Nelson, S. D., Sétamou, M. (2020): Root distribution and seasonal fluctuations under different grove floor management systems in citrus. – *Scientia Horticulturae* 272: 109364. DOI: 10.1016/j.scienta.2020.109364.
- [75] Soethe, N., Lehmann, J., Engels, C. (2006): The vertical pattern of rooting and nutrient uptake at different altitudes of a South Ecuadorian montane forest. – *Plant & Soil* 286(1-2): 287-299. DOI: 10.1007/s11104-006-9044-0.

- [76] Sparks, D. L., Page, A., Helmke, P., Loeppert, R., Soltanpour, P., Tabatabai, M., et al. (1996): Methods of Soil Analysis. Part 3. Chemical Methods. – Soil Science Society of America Inc., Madison, WI (No. 631.417/S736 V. 3).
- [77] Storer, D. A. (1984): A simple high sample volume ashing procedure for determination of soil organic matter. – Communications in Soil Science and Plant Analysis 15(7): 759-772. DOI: 10.1080/00103628.409367515.
- [78] Takahashi, K. (2010): Effects of altitude and competition on growth and mortality of the conifer *Abies sachalinensis*. – Ecological Research 25(4): 801-812. DOI: 10.1007/s11284-010-0710-6.
- [79] Thevathasan, N., Gordon, A. (2004): Ecology of tree intercropping systems in the North temperate region: experiences from southern Ontario, Canada. – Agroforestry Systems 61-62(1): 257-268. DOI: 10.1023/B:AGFO.0000029003.00933.6d.
- [80] Ugawa, S., Miura, S., Iwamoto, K., Kaneko, S., Fukuda, K. (2010): Vertical patterns of fine root biomass, morphology and nitrogen concentration in a subalpine fir-wave forest. – Plant & Soil 335(1-2): 469-478. DOI: 10.1007/s11104-010-0434-y.
- [81] Vicedo, O., Dilier. (2017): Response of radish seedlings (*Raphanus sativus*, L.) to different concentrations of ammoniacal nitrogen in absence and presence of silicon. – Agronomía Colombiana 35: 198-204. DOI: 10.15446/agron.colomb.v35n2.62772.
- [82] Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E. (2007): Let the concept of trait be functional! – Oikos 116: 882-892. DOI: 10.2307/40235131.
- [83] Vogel, J. G., Valentine, D. W., Ruess, R. W. (2005): Soil and root respiration in mature Alaskan black spruce forests that vary in soil organic matter decomposition rates. – Canadian Journal of Forest Research 35(1): 161-174. DOI: 10.1139/x04-159.
- [84] Vogt, K. A., Vogt, D. J., Palmiotto, P. A., Boon, P., O'Hara, J., Asbjornsen, H. (1995): Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. – Plant Soil 187: 195-219. DOI: 10.1007/BF00017088.
- [85] Wang, C. T., Cao, G. M., Wang, Q. L., Jing, Z. C., Ding, L. M., Long, R. J. (2007): Species composition of plant community in alpine meadow and biomass change along environmental gradient in Tibetan Plateau. – Sci China (Ser C) Life Sci 37(5): 585-592. DOI: 10.3969/j.issn.1674-7232.2007.05.014.
- [86] Wang, R. H., Li, J. R., Pan, G. (2018): Natural regeneration factors of *Abies georgei* var. *smithii* on Sejila Mountain. – Journal of Zhejiang A & F University (in Chinese).
- [87] Wang, W., Xu, W., Collett, J. L., Liu, D., Liu, X. (2019): Chemical compositions of fog and precipitation at Sejila Mountain in the southeast Tibetan Plateau, China. – Environmental Pollution 253: 560-568. DOI: 10.1016/j.envpol.2019.07.055.
- [88] Wilcox, D. A., Nichols, S. J. (2008): The effects of water-level fluctuations on vegetation in a Lake Huron wetland. – Wetlands 28: 487-501. DOI: 10.1672/07-129.1.
- [89] Williams, A., George, S., Birt, H., Daws, M. I., Tibbett, M. (2019): Sensitivity of seedling growth to phosphorus supply in six tree species of the Australian great western woodlands. – Australian Journal of Botany 67: 1-30. DOI: 10.1071/BT18247.
- [90] Witzgall, K., Vidal, A., Schubert, D. I., Hschen, C., Mueller, C. W. (2021): Particulate organic matter as a functional soil component for persistent soil organic carbon. – Nature Communications 12(1): 4115. DOI: 10.1038/s41467-021-24192-8.
- [91] Xia, F., Wang, X. A., Guo, H., Wang, S. X., Li, H. W., Fan, W. Y. (2012): Effects of Root Morphology on Seedling Growth of *Quercus liaotungensis* in Different Age Classes on Loess Plateau. – Chinese Agricultural Science Bulletin 28(10): 32-36 (in Chinese).
- [92] Xie, C. Q., Tian, M. X., Zhao, Z. R., Zheng, W. L., Wang, G. Y. (2015): Spatial point pattern analysis of *Abies georgei* var. *smithii* in forest of Sygera Mountains in Southeast Tibet, China. – Chinese Journal of Applied Ecology 26(6): 1617-1624 (in Chinese).
- [93] Xin, F. M., Liu, J. M., Yang, X. L., Zhao, K. T. (2017): Variation in leaf and fine root traits with altitude in *Abies georgei* var. *smithii* in Mt. Shergyla. – Acta Ecologica Sinica 37(8): 2719-2728. DOI: 10.5846/stxb201511162322.

- [94] Xu, Y., Zhang, Y., Li, W., Liu, W., Gu, X., Guan, Z., et al. (2019): Effects of tree functional diversity and environmental gradients on belowground biomass in a natural old-growth forest ecosystem. – Canadian Journal of Forest Research 49(12): 1623-1632. DOI: 10.1139/cjfr-2019-0254.
- [95] Yuan, Z. Y., Chen, H. (2010): Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. – Critical Reviews in Plant Sciences 29(4): 204-221. DOI: 10.1080/07352689.2010.483579.
- [96] Zhang, Z., Huang, M., Zhang, Y. (2018): Vertical distribution of fine-root area in relation to stand age and environmental factors in black locust (*Robinia pseudoacacia*) forests of the Chinese Loess Plateau. – Canadian Journal of Forest Research 48: 1-34. DOI: 10.1139/cjfr-2018-0149.
- [97] Zhou, C. N., Ren, Y. H., Ma, H. P., Guo, Q. Q. (2015): Research on soil organic carbon pool of typical natural dark coniferous forests in Sygara Mountains in Tibet. – Environmental Science & Technology 38(06): 1-7 (in Chinese).
- [98] Zhou, Y., Su, J. Q., Janssens, I. A., Zhou, G. S., Xiao, C. W. (2013): Fine root and litterfall dynamics of three Korean pine (*Pinus koraiensis*) forests along an altitudinal gradient. – Plant and Soil 374(1): 19-32. DOI: 10.1007/s11104-013-1816-8.

APPENDIX

Table A1. *F* and *p* values of *Abies georgei* var. *smithii* seedling characteristics

		Average plant height (cm)		Mean ground diameter (mm)		Mean diameter of fine roots (mm)		Mean length of fine roots (cm)	
		<i>F</i> -values	<i>p</i> -values	<i>F</i> -values	<i>p</i> -values	<i>F</i> -values	<i>p</i> -values	<i>F</i> -values	<i>p</i> -values
Variance analysis of different age groups at the same elevation	3815–3882 m	13.188	<i>p</i> < 0.001	14.328	<i>p</i> < 0.001	19.586	<i>p</i> < 0.001	25.165	<i>p</i> < 0.001
	3921–3992 m	9.251	<i>p</i> = 0.002	9.826	<i>p</i> < 0.001	7.403	<i>p</i> = 0.004	2.398	<i>p</i> = 0.119
	4009–4089 m	11.668	<i>p</i> < 0.001	9.080	<i>p</i> = 0.002	21.146	<i>p</i> < 0.001	6.894	<i>p</i> = 0.006
	4113–4194 m	18.161	<i>p</i> < 0.001	28.100	<i>p</i> < 0.001	8.764	<i>p</i> = 0.002	3.624	<i>p</i> = 0.044
	4207–4283 m	11.229	<i>p</i> < 0.001	64.428	<i>p</i> < 0.001	7.117	<i>p</i> = 0.005	12.163	<i>p</i> < 0.001
	4311–4379 m	15.432	<i>p</i> < 0.001	51.747	<i>p</i> < 0.001	7.868	<i>p</i> = 0.003	2.481	<i>p</i> = 0.111
Analysis of variance of the same age groups at different elevations	1	2.391	<i>p</i> = 0.100	1.662	<i>p</i> = 0.218	2.761	<i>p</i> = 0.069	0.398	<i>p</i> = 0.885
	2	18.389	<i>p</i> < 0.001	9.442	<i>p</i> < 0.001	13.148	<i>p</i> < 0.001	5.713	<i>p</i> = 0.006
	3	1.685	<i>p</i> = 0.212	0.956	<i>p</i> = 0.480	30.384	<i>p</i> < 0.001	1.104	<i>p</i> = 0.407
	4	0.273	<i>p</i> = 0.919	1.021	<i>p</i> = 0.447	4.100	<i>p</i> = 0.021	3.050	<i>p</i> = 0.052
	5	0.615	<i>p</i> = 0.690	0.462	<i>p</i> = 0.796	4.515	<i>p</i> = 0.015	0.706	<i>p</i> = 0.629

Table A2. Mean \pm SD value, F-value and P-value of root indexes of *Abies georgei* var. *smithii* seedlings

		HRL /cm		VRL/cm		FRB/g	
Mean \pm SD	Elevation /m (EL)						
	3815–3882	7.10 \pm 8.54a		7.39 \pm 3.81a		0.32 \pm 0.35a	
	3921–3992	5.73 \pm 7.68a		8.09 \pm 5.39a		0.23 \pm 0.37a	
	4009–4089	5.41 \pm 6.74a		5.37 \pm 3.54a		0.22 \pm 0.40a	
	4113–4194	7.65 \pm 5.91a		9.25 \pm 6.30a		0.37 \pm 0.68a	
	4207–4283	8.45 \pm 6.73a		7.06 \pm 4.08a		0.23 \pm 0.25a	
	4311–4379	8.64 \pm 6.60a		9.24 \pm 5.71a		0.31 \pm 0.39a	
	Age levels (AL)						
	1	0.83 \pm 0.53d		2.66 \pm 1.29d		0.01 \pm 0.01c	
	2	3.35 \pm 2.08cd		5.78 \pm 2.87cd		0.04 \pm 0.03c	
	3	6.39 \pm 4.57bc		7.39 \pm 2.97bc		0.13 \pm 0.09bc	
	4	9.34 \pm 5.87b		9.29 \pm 3.96b		0.33 \pm 0.21b	
	5	15.90 \pm 7.19a		13.55 \pm 4.99a		0.90 \pm 0.53a	
Variance analysis of different age groups at the same elevation		F-values	p-values	F-values	p-values	F-values	p-values
	3815–3882	11.234	p < 0.001	16.543	p < 0.001	27.509	p < 0.001
	3921–3992	4.217	p = 0.029	4.608	p = 0.022	9.015	p = 0.002
	4009–4089	8.043	p = 0.003	9.958	p = 0.002	5.797	p = 0.011
	4113–4194	3.401	p = 0.052	6.639	p = 0.007	5.022	p = 0.017
	4207–4283	5.541	p = 0.012	4.385	p = 0.026	29.630	p < 0.001
	4311–4379	5.333	p = 0.014	3.004	p = 0.072	5.833	p = 0.010
Analysis of variance of the same age groups at different elevations	1	1.359	p = 0.305	0.897	p = 0.513	0.929	p = 0.495
	2	4.179	p = 0.019	1.049	p = 0.433	9.214	p < 0.001
	3	2.059	p = 0.147	2.084	p = 0.137	8.222	p = 0.002
	4	2.321	p = 0.107	1.846	p = 0.178	2.474	p = 0.092
	5	0.517	p = 0.758	0.978	p = 0.469	0.779	p = 0.583

HRL: Horizontal root length; VRL: Vertical root length; FRB: Fine root biomass. 1: 1–2-year-old seedlings; 2: 3–4-year-old seedlings; 3: 5–6-year-old seedlings; 4: 7–8-year-old seedlings; 5: 9–10-year-old seedlings
 Different lowercase letters indicate significant differences among different elevations or age levels (p < 0.05)

Table A3. Contribution rate and *P* value of soil factors to HRL of *Abies Georgei* var. *smithii* seedlings at different age groups

HRL1			HRL2			HRL3			HRL4			HRL5		
Name	Contribution %	P	Name	Contribution %	P	Name	Contribution %	P	Name	Contribution %	P	Name	Contribution %	P
ST	32.5	0.018	NO ₃ ⁻ -N	19.5	0.048	AP	36.4	0.02	TK	19.7	0.046	NH ₄ ⁺ -N	36.3	0.018
AK	13.9	0.042	TOC	7.3	0.37	POC	17.5	0.066	NO ₃ ⁻ -N	17.8	0.042	SWC	22.7	0.024
TOC	17.9	0.052	POC	17.2	0.144	NH ₄ ⁺ -N	7.6	0.174	TP	11.6	12.9	POC	9	0.182
EOC	9.4	0.062	AK	7.7	0.31	ST	4.9	0.306	AP	4.9	0.302	TP	7.3	0.252
DOC	8.2	0.054	SWC	9.8	0.242	SWC	7.9	0.178	AK	4.3	0.326	TN	4.3	0.288
TK	11	0.206	TK	9.3	0.262	TOC	9	0.13	TOC	9.9	0.154	TOC	4.7	0.298
AP	4.6	0.24	ST	4.6	0.39	DOC	3.9	0.304	TN	9.4	0.108	ST	5.5	0.258
SWC	1.3	0.372	NH ₄ ⁺ -N	2.6	0.558	TK	5.2	0.24	DOC	3	0.4	AP	6.1	0.2
NO ₃ ⁻ -N	0.4	0.62	EOC	0.9	0.734	AK	2.1	0.484	SWC	7.9	0.12	EOC	2	0.494
POC	0.4	0.658	TN	1	0.726	EOC	2.2	0.438	EOC	5	0.194	AK	1.5	0.57
TN	0.3	0.744	TP	0	0	TP	2.1	0.492	NH ₄ ⁺ -N	2.3	0.322	TK	0.4	0.736
TP	< 0.1	0.876	AP	0	0	NO ₃ ⁻ -N	0.5	0.734	POC	2.5	0.342	DOC	< 0.1	0.992
NH ₄ ⁺ -N	< 0.1	0.978	DOC	0	0	TN	0.8	0.702	ST	0	0	NO ₃ ⁻ -N	0	0

HRL: Horizontal root length. 1: 1-2-year-old seedlings; 2: 3-4 years old seedlings; 3: 5-6 years old seedlings; 4: 7-8 years old seedlings; 5: 9-10 years old seedlings

Table A4. Contribution rate and *P* value of soil factors to VRL of *Abies Georgei* var. *smithii* seedlings at different age groups

VRL1			VRL2			VRL3			VRL4			VRL5		
Name	Contribution %	P	Name	Contribution %	P	Name	Contribution %	P	Name	Contribution %	P	Name	Contribution %	P
NO ₃ ⁻ -N	20	0.082	TK	35.3	0.02	TP	29	0.042	DOC	39.5	0.016	DOC	28.5	0.05
NH ₄ ⁺ -N	11.5	0.026	NO ₃ ⁻ -N	29.2	0.014	TK	13.4	0.132	TK	9.6	0.184	NH ₄ ⁺ -N	20.5	0.082
TN	16.3	0.062	TP	13.2	0.046	DOC	4.2	0.422	NO ₃ ⁻ -N	13.7	0.2	ST	20.5	0.036
TK	17	0.112	ST	6.2	0.122	ST	11.3	0.152	POC	3.3	0.454	POC	7.8	0.168
EOC	9.3	0.126	DOC	4.9	0.186	EOC	8.1	0.252	SWC	2.9	0.468	TN	4.5	0.246
DOC	8.3	0.202	NH ₄ ⁺ -N	5.2	0.152	TOC	11.6	0.13	TOC	1	0.7	TP	5.8	0.264
AP	4.7	0.336	EOC	2.3	0.272	SWC	3.7	0.37	AK	0.5	0.794	AK	2.9	0.384
TP	4	0.368	TOC	1.7	0.424	NO ₃ ⁻ -N	3.8	0.314	ST	0.2	0.876	TK	2.6	0.48
AK	4	0.406	AK	0.9	0.544	AK	4.8	0.32	TN	0.2	0.896	SWC	1.1	0.62
SWC	1.9	0.346	AP	0.6	0.612	TN	4	0.318	TP	0	0	EOC	0.8	0.662
TOC	2.7	0.282	TN	0.3	0.748	AP	1.2	0.606	AP	0	0	NO ₃ ⁻ -N	4.1	0.412
ST	0.3	0.698	POC	0.2	0.86	NH ₄ ⁺ -N	1.5	0.58	EOC	0	0	TOC	0.4	0.776
POC	0	0	SWC	< 0.1	0.896	POC	3.4	0.458	NH ₄ ⁺ -N	0	0	AP	0	0

VRL: Vertical root length. 1: 1-2-year-old seedlings; 2: 3-4 years old seedlings; 3: 5-6 years old seedlings; 4: 7-8 years old seedlings; 5: 9-10 years old seedlings

Table A5. Contribution rate and *P* value of soil factors to FRB of *Abies Georgei* var. *smithii* seedlings at different age groups

FRB1			FRB2			FRB3			FRB4			FRB5		
Name	Contribution %	P	Name	Contribution %	P	Name	Contribution %	P	Name	Contribution %	P	Name	Contribution %	P
TK	24.3	0.026	TK	52.9	0.008	ST	79.6	0.002	DOC	29.7	0.024	AP	32.8	0.032
SWC	8.3	0.09	ST	11	0.104	EOC	7.8	0.068	TK	24.6	0.014	AK	28.1	0.088
NO ₃ ⁻ -N	17.5	0.028	DOC	6.7	0.214	AP	4.5	0.15	AK	8.6	0.118	DOC	10.8	0.178
AK	20.7	0.086	NH ₄ ⁺ -N	4.8	0.26	DOC	1.1	0.46	AP	6.5	0.152	TP	3.7	0.42
DOC	10.9	0.22	AK	7.2	0.154	TOC	1.5	0.388	TP	5.9	0.152	NO ₃ ⁻ -N	2.1	0.544
EOC	3.4	0.256	POC	3.9	0.334	TN	0.2	0.744	TOC	7	0.14	POC	0.6	0.778
AP	3.7	0.2	TP	3.2	0.312	POC	0.5	0.692	EOC	3.9	0.212	TN	2.8	0.502
TOC	2.1	0.41	EOC	2.6	0.416	NO ₃ ⁻ -N	0.3	0.754	NO ₃ ⁻ -N	3.1	0.22	SWC	2.2	0.596
NH ₄ ⁺ -N	5.1	0.16	TOC	4.2	0.304	NH ₄ ⁺ -N	0.4	0.726	SWC	3.2	0.232	NH ₄ ⁺ -N	2.5	0.604
TN	2.7	0.292	AP	1.8	0.514	TP	< 0.1	0.882	POC	6.2	0.078	EOC	0.6	0.816
ST	0.9	0.534	NO ₃ ⁻ -N	0.9	0.648	SWC	< 0.1	0.89	ST	0.9	0.462	TOC	1.7	0.702
TP	0.2	0.78	TN	0.4	0.78	TK	0	0	TN	0.4	0.624	TK	0.4	0.86
POC	0.3	0.764	SWC	0	0	AK	0	0	NH ₄ ⁺ -N	0	0	ST	0	0

FRB: Fine root biomass.1:1-2-year-old seedlings; 2. 3-4 years old seedlings; 3:5-6 years old seedlings; 4:7-8 years old seedlings; 5:9-10 years old seedlings

Table A6. Mean \pm SD value, *F*-value and *p*-value of soil factors at each elevation

	3815–3882m	3815–3882m	3815–3882m	3815–3882m	3815–3882m	3815–3882m	<i>F</i> -values	<i>p</i> -values
AP	1.84 \pm 0.48a	1.39 \pm 0.24a	1.55 \pm 0.77a	1.54 \pm 0.21a	2.18 \pm 0.37a	2.06 \pm 0.5a	1.377	<i>p</i> = 0.299
AK	0.09 \pm 0.02a	0.06 \pm 0.01a	0.07 \pm 0.01a	0.07 \pm 0.02a	0.07 \pm 0.01a	0.08 \pm 0.04a	0.496	<i>p</i> = 0.773
NH ₄ ⁺ -N	7.17 \pm 0.73a	6.49 \pm 0.78a	5.11 \pm 0.43a	3.99 \pm 1.83a	6.73 \pm 1.76a	5.1 \pm 2.81a	1.707	<i>p</i> = 0.207
NO ₃ ⁻ -N	0.97 \pm 0.64c	2.47 \pm 0.77bc	2.71 \pm 0.13ab	2.23 \pm 0.77bc	4.13 \pm 0.29a	2.24 \pm 0.64bc	8.884	<i>p</i> = 0.002
TP	0.42 \pm 0.08b	0.73 \pm 0.07a	0.59 \pm 0.03ab	0.52 \pm 0.02b	0.72 \pm 0.11a	0.59 \pm 0.05ab	8.564	<i>p</i> = 0.002
TK	5.53 \pm 0.45b	8.13 \pm 0.53a	7.97 \pm 0.54a	8.46 \pm 0.6a	8.82 \pm 0.71a	9.19 \pm 1.02a	11.244	<i>p</i> < 0.001
TN	2.21 \pm 0.45a	3.56 \pm 0.84a	2.79 \pm 0.18a	2.73 \pm 0.87a	4.08 \pm 0.14a	3.97 \pm 2.14a	1.626	<i>p</i> = 0.226
TOC	45.83 \pm 7.5a	52.86 \pm 9.26a	38.38 \pm 3.19a	34.52 \pm 5.59a	45.68 \pm 3.09a	53.07 \pm 23.29a	1.378	<i>p</i> = 0.299
SWC	0.31 \pm 0.04b	0.39 \pm 0.01ab	0.37 \pm 0.02ab	0.37 \pm 0.01ab	0.4 \pm 0.01ab	0.43 \pm 0.07a	3.711	<i>p</i> = 0.029
ST	14.6 \pm 0.5a	9.5 \pm 0.4cd	9.5 \pm 0.6cd	10.87 \pm 0.57b	8.83 \pm 0.12d	10.53 \pm 0.35bc	63.241	<i>p</i> < 0.001
EOC	15.06 \pm 3.46a	23.27 \pm 4.61a	14.35 \pm 1.77a	12.92 \pm 3.69a	16.97 \pm 1.48a	22.1 \pm 13.35a	1.431	<i>p</i> = 0.282
DOC	48.29 \pm 8.57b	186.77 \pm 41.99a	190.51 \pm 44.37a	235.17 \pm 49.43a	146.46 \pm 17.66ab	147.4 \pm 42.5ab	8.654	<i>p</i> = 0.002
POC	18.68 \pm 2.85a	17.05 \pm 6.62a	10.99 \pm 3.57a	19.7 \pm 12.97a	27.84 \pm 5.99a	47.63 \pm 35.36a	1.982	<i>p</i> = 0.153

Different lowercase letters indicate significant differences among different elevations (*p* < 0.05)