



Response of cone and seed traits diversity and germination characteristics of Minjiang fir to elevations and crown directions on the eastern Qinghai-Tibet Plateau

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Abstract In the process of secondary forests restoration on the eastern Qinghai-Tibet Plateau, the regeneration of Minjiang fir (*Abies fargesii* var. *faxoniana*) is of critical importance. Key challenges in regeneration include securing a stable seed supply and ensuring seedling survival; however, research on the seed ecology of these species remains limited. This study collected cones and seeds of Minjiang fir from seven sites distributed along four elevations on the eastern Qinghai-Tibet Plateau. We compared the coefficient of variation and diversity, conducted multiple comparisons, examined correlations, and analyzed seed vigor and germination across elevations and crown directions. The results showed that: (1) Cones length and

weight were 5.98 ± 1.36 cm and 29.06 ± 12.39 g. Seed size was 11.2 ± 1.9 mm, and the weight of 1,000 seeds was 8.86 ± 2.31 g. Seed vigor averaged 19.05% and germination rate was 17.61%. (2) With increasing elevation, the morphological traits of cones and seeds first increased, peaked at 3,300–3,600 m, and then decreased. Trait variations were less pronounced than at other elevations, and diversity analysis revealed weaker differentiation, with more stable seed trait expression. Furthermore, cone and seed traits near the timberline areas are significantly smaller than those in adjacent lower elevation zones. The 3,300–3,600 m elevation zone appears to be the most suitable habitat for Minjiang fir. (3) Seed vigor and germination rate followed unimodal distribution patterns. Seeds at 3,900 and 3,300 m germinated faster than 3600 m, whereas seeds at 3,000 m took the longest time to initiate germination. Seeds at higher elevations exhibited faster post-initiation germination but later initial germination and a lower final germination rate. (4) Seed vigor and germination rate are positively correlated with cone length, cone weight, seed length, seed weight, tree height, diameter at breast height, and crown direction, and negatively correlated with elevation and the number of seeds per cone. Cone weight had the highest contribution to seed vigor and germination (21.5%), followed by elevation

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(18.39%). Minjiang fir growing on the sunny side of the crown exhibited better cone and seed traits, including larger, plumper seeds. This study validates the mid-elevation peak pattern of Minjiang fir with increasing elevation and can help understand the regeneration of coniferous trees in high-mountain areas.

Keywords *Abies fargesii* var. *faxoniana* · Cone and seed · Elevation · Crown direction · Diversity analysis · Germination

Introduction

Seeds are vital to the continuity of plant species, the stability of ecosystems, and the regeneration and restoration of forests. Forest regeneration begins with seeds, and understanding how their characteristics vary under different habitat conditions is fundamental for explaining regeneration success. Recent studies have examined differences in cone and seed traits along various altitudinal gradients, revealing notable variations. For instance, *Abies chensiensis* cones develop at lower elevations and are of lower quality at higher elevations (Sun 2004; Zhang et al. 2005); the length, width, thickness, and thousand-seed mass of seeds of *Abies ferreana* seeds are significantly larger at low elevations compared to higher elevations (Wang et al. 2023b). Mid and low-elevation cones and seeds in the Sejila Mountain *Abies georgei* var. *smithii* forests in Southeastern Xizang were larger, with higher thousand-seed mass, seed yield, and fullness than those at higher elevations (Luo et al. 2010). In Western Sichuan, the length, width, and mass of *Picea asperata* seeds exhibit a negative correlation with elevation, with seed size and mass decreasing with increasing elevation (Luo et al. 2003). Among the four naturally distributed populations on the Greek island of Crete, the mean values for *Pinus brutia* cone and seed traits reached their peak in mid- to high-elevation regions (Dangasuk and Panetsos 2004). *Pinus patula* consistently outperformed all *Pinus tecunumanii* populations in cone and seed yield at high elevations, while at low elevations, *Pinus oocarpa* did not significantly differ from *Pinus tecunumanii* in cone and seed yield (Nyoka and Tongoona 2000); in *Pinus monticola*, seed scale width and seed scale length significantly varied with elevation, whereas other traits, such as seed weight, also exhibited elevational variation but did not show significant differences among elevations (Barnes 1967). Usually, in coniferous species, cone and seed traits generally correlate negatively with increasing elevation, with morphological features declining at higher elevations (Sun 2004; Körner 2003). Nevertheless, the effects of elevation on conifer seed traits show marked species-specific and geographic variability. This variability arises from both intra- and interspecific differences in how elevations

influence seed traits, primarily due to differences in parent tree growth and microhabitat heterogeneity along altitudinal gradients. However, for species of *Abies*, studies of seed ecology remain limited due to the mast-seeding phenomenon in seed yield (Guan 1982) and the difficulty of cone collection, as seed scales readily detach and disperse once the cones mature. While former studies mainly focused on representative morphological traits of conifers, a notable gap remains in understanding the altitudinal ecological range of fruiting traits in dominant coniferous tree species across the Qinghai-Tibet Plateau.

Crown direction factors essentially regulate seed physiological and ecological traits, including seed yield and seed quality. Recent studies have examined cone and seed trait differences among crown directions, revealing the specific effects on cone and seed development in various tree species. Xie et al. (1998) and Tang et al. (2001) reported higher cone yields on the sunny side of the crown in *Cathaya argyrophylla* and *Abies yuanbaoshanensis*. In a study of *Abies georgei* var. *smithii* in the Sejila Mountains of Xizang, Luo et al. found that firs had more cones on the sunny side of their tree crowns than on the shady side (Luo et al. 2010). In a study of *Pinus bungeana* by Wang et al. in Hui County, Gansu Province, different crown directions affected fruiting, with cones and more seeds growing better on the sunny side of the crown than on the shady side (Wang 2002), consistent with the findings in the seeds of *Pinus massoniana* (Ye and Dai 1994). Previous research has mainly focused on differences in fruit yield among crown directions, which significantly affect seed quantity. However, comprehensive seed quality assessment, including seed vigor and germination, across tree crown directions (sunny and shady sides), remains scarce.

Cone and seed traits are usually more developed at lower elevations than at higher elevations, and crown directions significantly affect firs because of differences in light supply and temperature conditions (Wang et al. 2023a, b). Those studies indicate that the quantity and quality of cones and seeds vary considerably in response to environmental factors along altitudinal gradients, reflected in phenotypic, biochemical composition, physiological functions, and other traits (Wyllie-Echeverria et al. 2003; Wang et al. 2005). However, conifer species respond inconsistently to environmental differences in elevations, highlighting the need to examine Minjiang fir cone and seed traits across elevation gradients.

The upper Minjiang River lies on the eastern edge of the Qinghai-Tibet Plateau. This region lies within the “Two Screens and Three Belts” ecological barrier area, which is crucial for water conservation and biodiversity protection in the Chengdu Plain and the upper Yangtze River (Bao et al. 1995; Liu et al. 2009). Minjiang fir (*Abies fargesii* var. *faxoniana*) is the dominant and zonal tree species, with exceptional water-conservation, transfer, and storage

capacity in the subalpine region, in the upper reaches of the Minjiang River (Cui et al. 2009). The regeneration of Minjiang fir is closely linked to the success of secondary forest restoration in this region, with seed traits playing a crucial role. It is a critical scientific and technological issue that urgently requires a solution in seed ecology research in this region. Seed bioecological traits of dominant tree species are key to understanding their adaptability and survival strategies. However, existing research primarily addresses Minjiang fir breeding and seedling nursery technology (Ma and Yin 1998; GB/T6001 2022), while the bioecological traits of cones and seeds, as well as their response to topographic variations in growth conditions, remain poorly understood. Therefore, detailed studies on the bioecological traits of Minjiang fir seeds are urgently needed to inform ecological restoration efforts.

In this study, we investigated Minjiang fir cones and seeds to assess the effects of elevation and crown direction on their bio-ecological traits. We propose three key scientific questions to address the knowledge gaps mentioned above: (1) How do elevation and crown direction affect seed traits diversity and germination? (2) How does the habitat edge of the timberline ecological zone affect cone and seed yield? (3) Which elevation ranges are suitable for cone and seed yield? This research may help clarify the ecological adaptation of Minjiang fir. It may also deepen our understanding of conifer reproduction strategies and provide knowledge for forest restoration and management (Table 1).

Materials and methods

Research area

The study area is situated in the Miyaluo Forest Region (31°24′–31°55′ N, 102°35′–103°4′ E, 2,200–5,500 m), located in Li County, Sichuan Province (Fig. 1). This region represents the transition zone between the Qinghai–Tibet Plateau and the Sichuan Basin. The average annual temperature ranges of 6–12°C, and annual

precipitation ranges from 600 to 1,100 mm, while annual evaporation ranges from 1,000 mm to 1,900 mm. The timberline in this area is approximately 4,000–4,200 m. The climate is characterized by cold winters and cool summers, with marked elevational and topographic effects on regional conditions. Vegetation in the Miyaluo Forest Region shows distinct vertical zoning (Liu et al. 2022). In the subalpine dark coniferous forests, which are mainly distributed at elevations between 2,400 and 4,200 m, the main dominant tree species is Minjiang fir. From the 1950s to 1998, western Sichuan's dark-coniferous primary forests, dominated by fir (*Abies* spp.) and spruce (*Picea* spp.), underwent large-scale logging. Since 1998, ecological initiatives and forest areas have implemented ecological projects, including the Natural Forest Resource Protection and the Grain for Green Projects.

Parent-tree selection and cone collection

In October 2023, we conducted a study along an altitudinal gradient, starting at 3,000 m, with sampling intervals of 300 m and a 50 m buffer for both upper and lower sampling sites. Sampling sites were situated on the shady slopes of Big Gully in the Miyaluo Forest Region (2,750–4,100 m), including four sites at 3,000, 3,300, 3,600, and 3,900 m, and on the shady slopes of Tenth Gully (3,250–4,000 m), with three sampling sites at 3,300, 3,600, and 3,900 m (Fig. 1).

Six to nine healthy parent trees (≥ 22.5 cm diameter at 1.3 m of tree height) were selected from each altitudinal gradient for cone and seed collection, with collection performed by climbing up to tree crowns and using pruning shears. A minimum distance of 30 m was maintained between parent trees. Sampling was conducted on both the shady and sunny sides of the crown, with 10 to 20 intact and mature cones collected from each side. A total of 1,539 mature cones were collected (Table 1). The collected cones were wrapped in cling film, placed in envelopes, and transported

Table 1 Basic information of the cone samples

Sample site	Elevation (m)	Sample size of the parent tree	Average DBH (cm)	Sample size of cones	Ranges of latitude and longitude (°)
Big Gully	2,950–3,050	6	44.07	189	31.6322° N–31.6554° N, 102.8008° E–102.8232° E
	3,250–3,350	6	43.88	169	31.8237° N–31.8418° N, 102.6821° E–102.6881° E,
	3,550–3,650	8	39.00	285	31.8528° N–31.8533° N, 102.6962° E–102.6965° E
	3,850–3,950	6	33.13	255	31.6211° N–31.6217° N, 102.7948° E–102.7955° E
Tenth Gully	3,250–3,350	7	50.67	196	31.8206° N–31.8243° N, 102.6724° E–102.6823° E
	3,550–3,650	7	45.56	150	31.8214° N–31.8224° N, 102.6754° E–102.6785° E
	3,850–3,950	9	33.31	295	31.8552° N–31.8556° N, 102.6916° E–102.6924° E

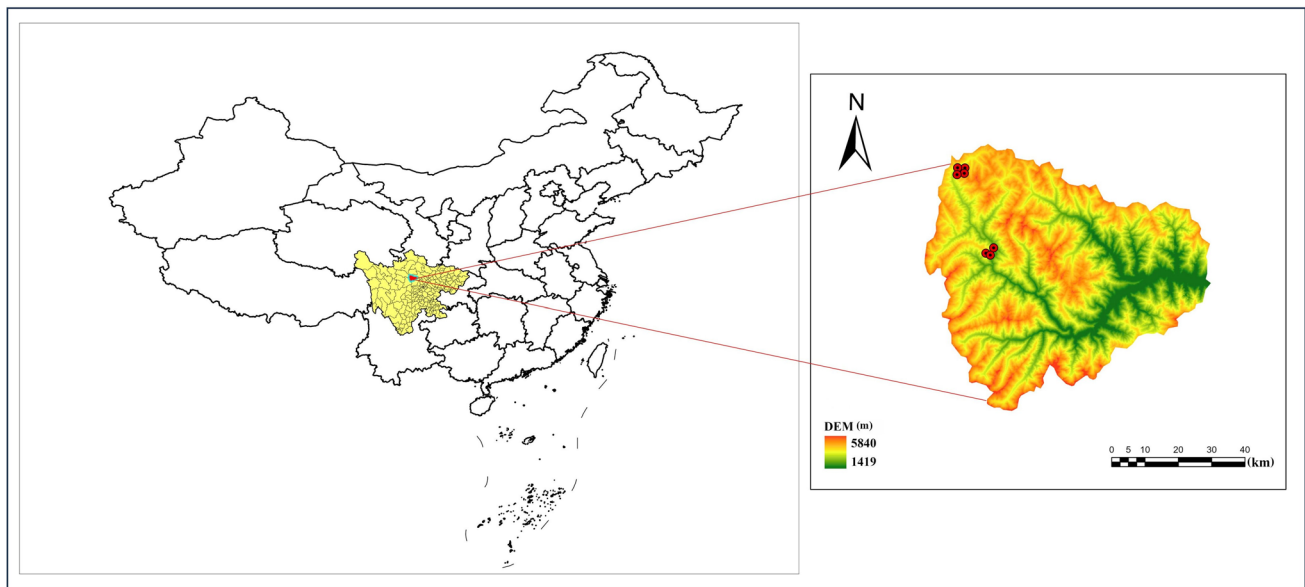


Fig. 1 Location of the study area and sampling sites

to the laboratory for measurement of relevant traits before natural drying.

Cone and seed traits examination

After cone collection, cone length, width, and thickness ($n = 1539$) were measured using a vernier caliper with an accuracy of 0.01 mm. Cone weight was measured using an electronic balance with an accuracy of 0.001 g. Subsequently, the number of seeds per cone was counted for the sampled cones ($n = 840$).

After one month of natural drying and maturation in a cool and dry place, the cones naturally dehisced, releasing their seeds. For each altitudinal gradient in the two sample sites, ten cones were randomly selected from both the sunny and shady sides, yielding a total of 140 cones. The seeds were then separated from the seed scales using a sieve. Six intact seeds and six intact seed scales were randomly selected from each cone for photography, totaling 840 seeds. The thickness of the seeds and seed scales was measured with a vernier calliper with an accuracy of 0.01 mm. The length and width of the seeds, seed wings, and seed scales were measured using ImageJ software (V1.54 g). Additionally, 100 seeds were randomly selected from each cone and weighed, resulting in 140 datasets of seed mass. The weight of 1,000 seeds was calculated based on the 100-seed method.

Determination of seed vigor and germination

Seed vigor was assessed using TTC (2,3,5-triphenyltetrazolium chloride) staining: seeds were categorized into four

groups ($n = 150$ seeds/group) based on their original elevation gradients. Seeds were soaked in water at 25 °C for 12 h. These seeds were dissected longitudinally to screen for embryo-bearing seeds. Seeds were stained with 0.5%–1% TTC and incubated at 35 °C for 4–6 h. Vigor was determined from staining patterns: seeds with red-stained radicles were viable, while unstained or partially stained seeds were non-viable. Each experiment was repeated six times.

Seed germination was tested using seeds from both source locations. Seeds were randomly divided into four sets of 100 per elevation (total number = 400). All seeds were first sterilized with a 0.2% K_2MnO_4 solution for 20 min at a constant temperature of 25 °C, followed by three rinses with distilled water. They were subsequently placed in 6 cm Petri dishes lined with river sand and moistened by adding 3 mL of distilled water. During incubation, 1–2 mL of water was added daily, and germination was recorded every 24 h. The experiment was repeated three times.

Statistical analysis

The lengths and widths of seeds and seed scales were measured using ImageJ (version 1.54 g). We used IBM SPSS Statistics 27 to calculate the mean value, standard deviation (SD), and multiple comparisons of morphological characteristics of seeds and cones across different regions, elevations, and crown directions, as well as to calculate seed vigor and germination rates across different elevations. We adopted the one-way analysis of variance (ANOVA), LSD, and independent-samples t-tests to analyze cone and seed traits. We used the redundancy analysis (RDA) to quantify

the effects of environmental factors on seed length and seed weight. The relative contributions of respective seed length and seed weight were further analyzed using a random forest model (Lai et al. 2022). Seed germination curves were fitted with a logistic model (Tudela-Isanta et al. 2018). Elevation acclimatization of cones and seeds was predicted using a Generalized Additive Model (GAM) (Wood 2017), and the moderating effect of crown direction on the pattern of elevation response of cones and seed traits was analyzed using a Linear-Mixed Model (LMM). Using Origin 2022, we generated all the figures.

The data standardized seed phenotypic traits had different scales. Seed trait indicators were classified at 10 levels (with a difference of 0.5 δ between each level) for statistical analysis, with level $1 < X - 2\delta$, $X - 2\delta \leq$ level $2 < X - 1.5\delta$, $X - 1.5\delta \leq$ level $3 < X - \delta$, $X - \delta \leq$ level $4 < X - 0.5\delta$, $X - 0.5\delta \leq$ level $5 < X$, $X \leq$ level $6 < X + 0.5\delta$, $X + 0.5\delta \leq$ level $7 < X + \delta$, $X + \delta \leq$ level $8 < X + 1.5\delta$, $X + 1.5\delta \leq$ level $9 < X + 2\delta$, level $10 \geq X + 2\delta$. X is the mean of the trait variable, and δ is the standard deviation in each level. The trait diversity (TD) of seeds was then calculated using the Shannon–Wiener index.

Shannon–Wiener index:

$$H' = - \sum_{k=1}^{10} p_k \ln(p_k) \quad (1)$$

where k is the number of phenotypic levels for a given trait, and P_k is the number of copies of material within level k of a trait as a percentage of the total number of copies.

Results

Basic traits of Minjiang fir cones and seeds

The maximum cone size (8.01 cm length, 3.63 cm width) and cone weight (51.19 g) were recorded at 3,300 m, accompanied by the highest seed quality (11.64 g per thousand seeds) and reproductive yield (667 seeds per cone). At 3,900 m, the length of cones decreased to 4.80–5.31 cm, the cone weight to 19.00–30.57 g, and the weight of 1,000 seeds to 5.98 g. At 3,900 m, cone width (2.89–3.37 cm), thickness (2.89–3.36 cm), and seed mass (6.63–10.44 g) were significantly higher on the sunny side than on the shady side, where the width was 2.80 cm, the thickness was 2.82 cm, and the weight of 1,000 seeds was 5.98 g. Seed traits also mirrored this pattern, varying unimodally with elevation and being greater on the sunny side than the shady side (Supplementary Appendices 1 and 2).

The RDA results showed that the explanatory rate of the variables was 35.3%, with 26.23% and 9.07% for the first and second axes, respectively (Fig. 2A). Seed vigor and

germination were positively correlated with crown direction, diameter at breast height (DBH), cone length, cone weight, parent tree height, seed length and seed weight, and negatively correlated with elevation and number of seeds per cone (Fig. 2A). Among the independent contributions of the nine factors, cone weight (21.50%) contributed the most to seed vigor and germination. In addition to the effects of seeds and cones themselves, elevation contributed the most to seed vigor and germination rate (18.39%), which proved that among the external environmental factors, elevation had a greater effect on seed morphological characteristics (Fig. 2C). The one-way importance histogram (Fig. 2C) showed relatively more potent effects of cone weight (CW), elevation (AL), and seed thousand kernel weight (SW) on seed size/weight, and weaker effects of tree height (TH) and crown direction (CD). In addition, by PCA analysis, the first and second principal components cumulatively explained 66.5% of the variance (PC1 = 45.9%, PC2 = 20.6%), and the top five factors accounted for more than 85% of the variance. Meanwhile, the elliptical confidence intervals between the four elevation gradient groups showed a precise gradient distribution, and this continuous separation along the principal component axes indicated that elevation was one of the key factors affecting seed traits (Fig. 2B).

Morphological traits of cones and seeds varied with elevation

At the Big Gully site, all traits except seeds per cone showed an increasing trend from 3,000 to 3,300 m, followed by a decreasing trend from 3,300 to 3,900 m. Significant differences in cone traits were observed among the four elevations ($p < 0.05$). The number of seeds per cone at 3,000 m did not differ significantly from 3,300 m ($p > 0.05$), nor did 3,600 m vary from 3,900 m ($p > 0.05$). However, the number of seeds per cone was significantly greater at lower elevations than at higher elevations ($p < 0.05$). At Tenth Gully, the cone length and the cone weight increased, peaking at 3,300 m, then decreased at 3,900 m with increasing elevation. Significant cone length and weight differences were observed between elevations ($p < 0.05$). In contrast, the width and thickness of the cones increased with elevation, but these differences were not statistically significant ($p > 0.05$) (Fig. 3).

At Big Gully site, seed scale length had an increasing trend from 3,000 to 3,300 m, a decreasing trend from 3,300 to 3,600 m, and a smaller increasing trend from 3,600–3,900 m, except for the no significant difference between 3,600 and 3,900 m ($p > 0.05$), there was a significant difference among 3,000 to 3,600 m ($p < 0.05$). Except for seed scale length, all other seed traits exhibit an upward trend from 3,000 to 3,300 m and from 3,300 to 3,900 m, indicating a decreasing trend with increasing elevation. Seed scale thickness and seed wing width differed significantly

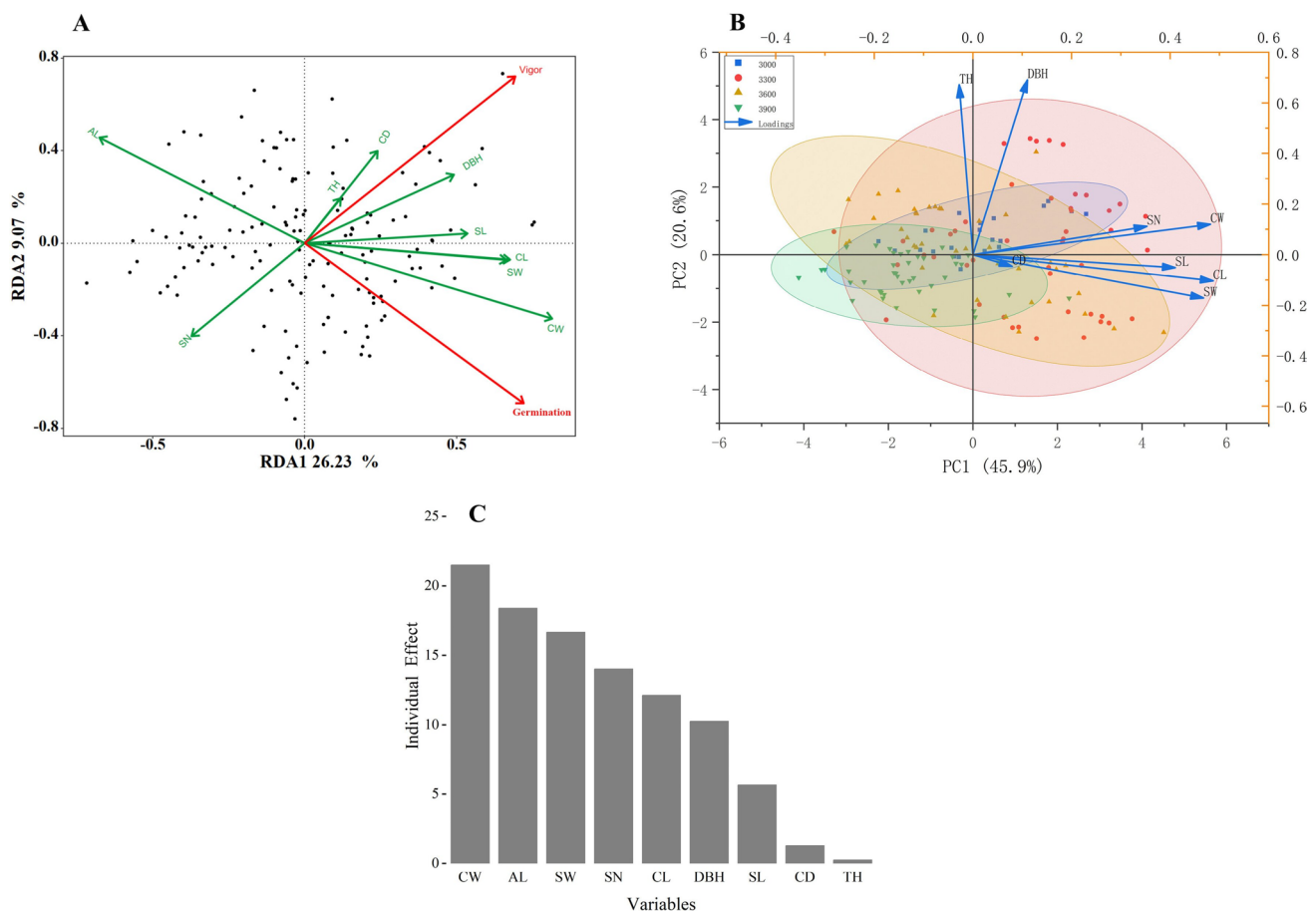


Fig. 2 Redundancy analysis (RDA) **A** and principal component analysis (PCA) **B** of factors for seed vigor and germination of Minjiang fir and the relative importance of individual factors **C**. Note: AL, elevation; 1000 SW, weight of 1,000 seeds; SL, seed length; CW, cone

weight; CL, cone length; SN, number of seeds per cone; DBH, diameter at breast height of the parent tree; TH, height of the parent tree; CD, crown direction

among elevations ($p < 0.05$). No significant differences were observed in seed scale width, seed wing length, seed size, seed length, or seed width between 3,600 and 3,900 m ($p > 0.05$), nor were there significant differences in seed thickness at 3,000, 3,600, and 3,900 m ($p > 0.05$) (Fig. 4).

At the Tenth Gully sample site, seed wing length, width, and seed scale width and thickness increased with elevation. Significant differences were in seed scale width, seed wing length, and seed wing width between elevations ($p < 0.05$). However, some elevations had no significant differences, such as seed scale thickness between 3,300 and 3,600 m ($p > 0.05$). Additionally, seed scale length, width, thickness, and size all increased with elevation. No significant differences were observed between 3,600 and 3,900 m for these traits (seed scale length, seed length, width, thickness, and seed size) ($p > 0.05$) (Fig. 4). The characteristics of cones and seeds varied at the same elevation in different sites. Still, at the mid-elevation of 3,300 to 3,600 m, all the traits of seeds and cones were significantly larger than those traits at other elevations.

The GAM analysis revealed that all seed cone traits exhibited a non-linear response pattern with increasing elevation. Simulation results for cone width and cone thickness showed a slight upward trend near 3,900 m, whereas the weight of 1,000 seeds and cone thickness showed lower fitness (Fig. 5).

Seed traits reached their peak in the 3,300–3,600 m interval. Seed wing length ($R^2 = 0.373$) and width ($R^2 = 0.403$) had significantly lower model explanatory power than other traits, but their confidence interval bandwidths showed less fluctuation with elevation. Seed thickness was associated with lower fitness ($R^2 = 0.173$). Additionally, the decreasing trend of seed scale length, width, thickness, and seed size slowed as elevation approached 3,900 m (Fig. 6).

Differences between crown direction and the morphological traits of the cones and seeds

Cone width and thickness on the sunny side were significantly larger than those traits on the shady side ($p < 0.05$).

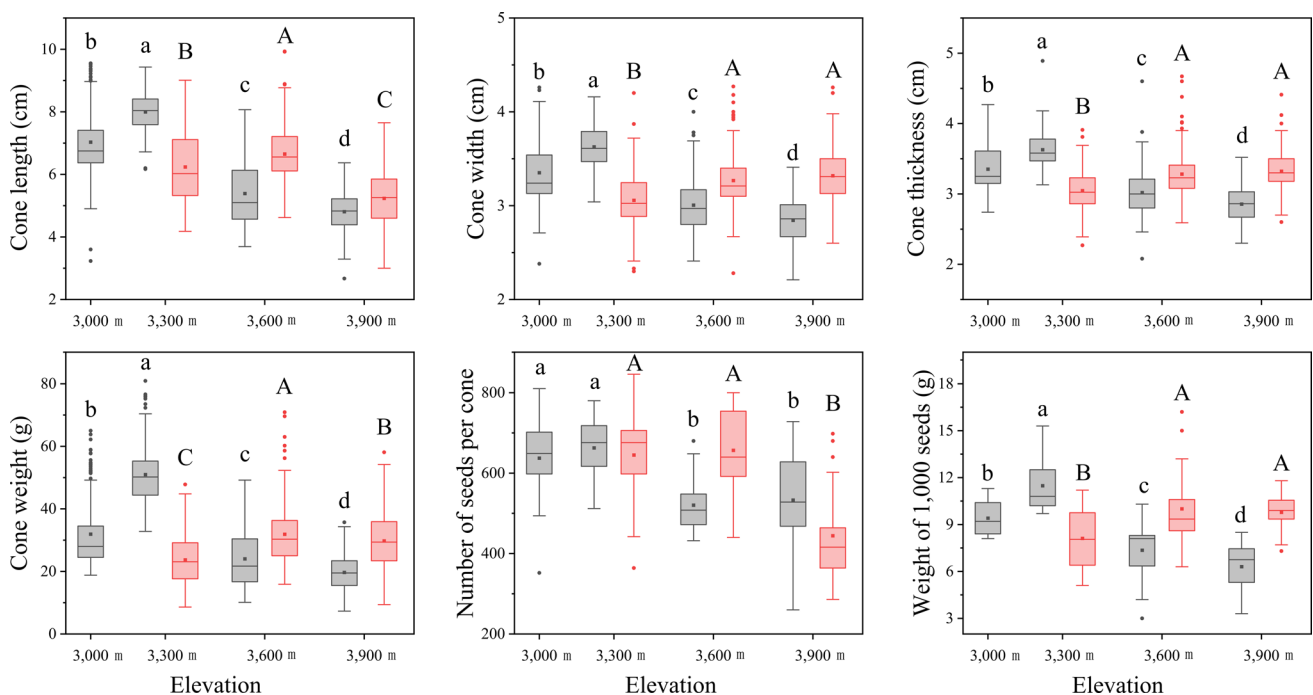


Fig. 3 Comparison of the morphological traits of cones at different elevations. Note: Morphology traits refer to cone length, width, thickness, weight, number of seeds per cone, and weight of 1,000 seeds. Lowercase letters in each trait indicate the significant difference

between the four elevations in the Big Gully sample site ($p < 0.05$); uppercase letters indicate significant differences between the three elevations in the Tenth Gully sample site ($p < 0.05$)

However, there were no significant differences between the sunny and shady sides of cone length, cone weight, weight of 1,000 seeds, and the number of seeds per cone ($p > 0.05$) (Supplementary Appendix 3). Seed length exhibited significant differences between the sunny and shady sides ($p < 0.01$). Significant differences were also observed in seed scale length, seed scale thickness, seed wing length, seed size, and seed width among the directions ($p < 0.05$), with seeds on the sunny side significantly larger than those on the shady side. However, there were no significant differences in seed scale width, seed wing width, or seed thickness ($p > 0.05$) (Supplementary Appendix 4).

LMM analysis revealed that with increasing elevation, although most cone and seed traits did not show significant divergence ($p > 0.05$) between crown directions, the decrease in seed size with elevation was significantly slower on the sunny side than on the shady side ($p < 0.01$) (Fig. 7). Similarly, the decline in cone width along the elevation gradient was less pronounced on the sunny side ($p < 0.05$). In contrast, the weight of 1,000 seeds increased slightly on the sunny side but decreased on the shady side with elevation ($p < 0.01$) (Fig. 7).

Traits of cones and seeds in timberline and below-timberline ecotones

All the traits of cones (cone length, cone width, cone thickness, cone weight, number of seeds per cone, weight of 1,000 seeds) in the timberline area were significantly lower than those in the below-timberline areas ($p < 0.05$) (Fig. 8).

All the trait indices of seeds in the timberline area were lower than those in the below-timberline area. Except for seed wing length and seed thickness, all other seed traits (seed length, width, size; seed scale length, width, thickness; seed wing width) differed significantly between timberline and below-timberline ecotones ($p < 0.01$). Seed wing length also showed a significant difference ($p < 0.05$), while seed thickness showed no significant difference ($p > 0.05$) (Fig. 9).

Seed vigor and germination characteristics with increasing elevations

The seed vigor of Minjiang fir was 19.05%, and the laboratory germination rate was 17.61%. Both seed vigor and germination rate of Minjiang fir showed unimodal distributions across different elevation gradients, with peaks at 3,300 m. The median seed vigor of the 3,000 m group was 18%, which rose to the peak of 22% in the 3,300 m group, stayed at 21%

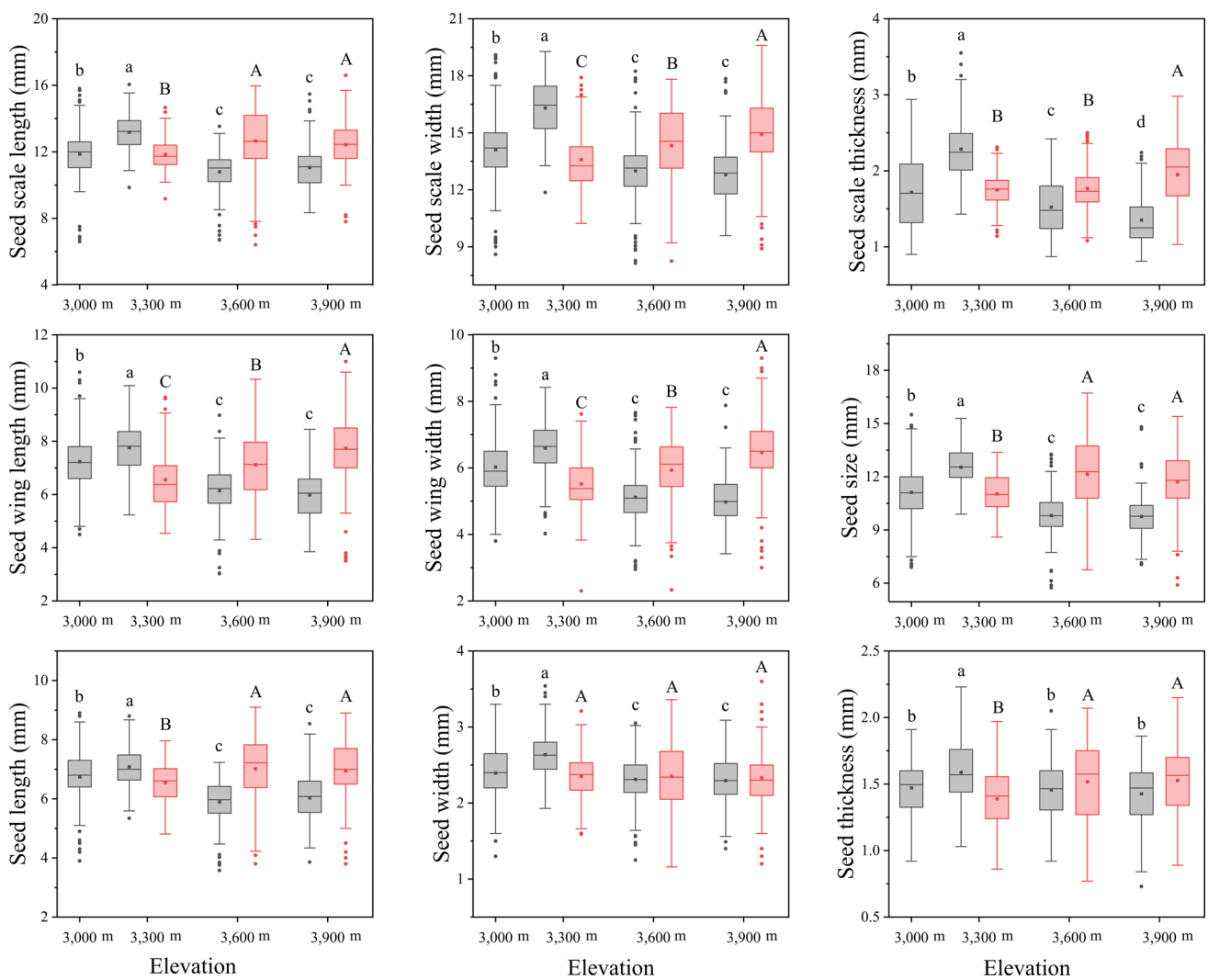


Fig. 4 Comparison of changes in seed morphology traits at different elevations. Note: Morphology traits refer to seed length, width, thickness, and size; seed scale length, width, and thickness; and seed wing length and width. Lowercase letters in each trait indicate the signifi-

cant difference between the four elevations in the Big Gully sample site ($p < 0.05$); uppercase letters indicate significant differences between the three elevations in the Tenth Gully sample site ($p < 0.05$)

in the 3,600 m group, and decreased to 16% in the 3,900 m group (Fig. 10B). The average germination rate was 15% in the 3,000 m group, reaching a peak of 20% in the 3,300 m group, 18% in the 3,600 m group, and dropping to 15% in the 3,900 m group. The superimposed trend line in the graph clearly shows a single peak in germination rate at 3,300 m (Fig. 10A). The seed germination rate (17.61%) was slightly lower than the vigor (19.05%).

The germination curves of Minjiang fir seeds at all four altitudinal gradients showed a typical S-shaped curve, and the logistic goodness of fit (R^2) was higher than 0.98. Among them, the t_{50} value of the germination curve at 3,000 m was 17.5 d; the t_{50} value of the germination curve at 3,900 m was 15.0 d; the t_{50} value of the germination curve at 3,600 m was 15.8 d; and the fastest germination process was shown at

3,900 m, with a t_{50} value of 14.6 d. The data showed that the 3,900 m gradient took the shortest time for seed germination to reach the t_{50} point ($t_{50} < 15$ d), followed by the 3,300 m and 3,600 m gradients, whereas the 3,000 m gradient took the longest time (Fig. 10C).

Variation of traits in cones and seeds at different elevations

The coefficient of variation (CV) for the weight of 1,000 seeds, seed scale thickness, seed wing length, seed wing width, and seed scale width was highest at 3,900 m. In contrast, the CV for cone length, cone thickness, number of seeds per cone, seed thickness, seed size, seed length, seed width, and seed scale length peaked at 3,600 m.

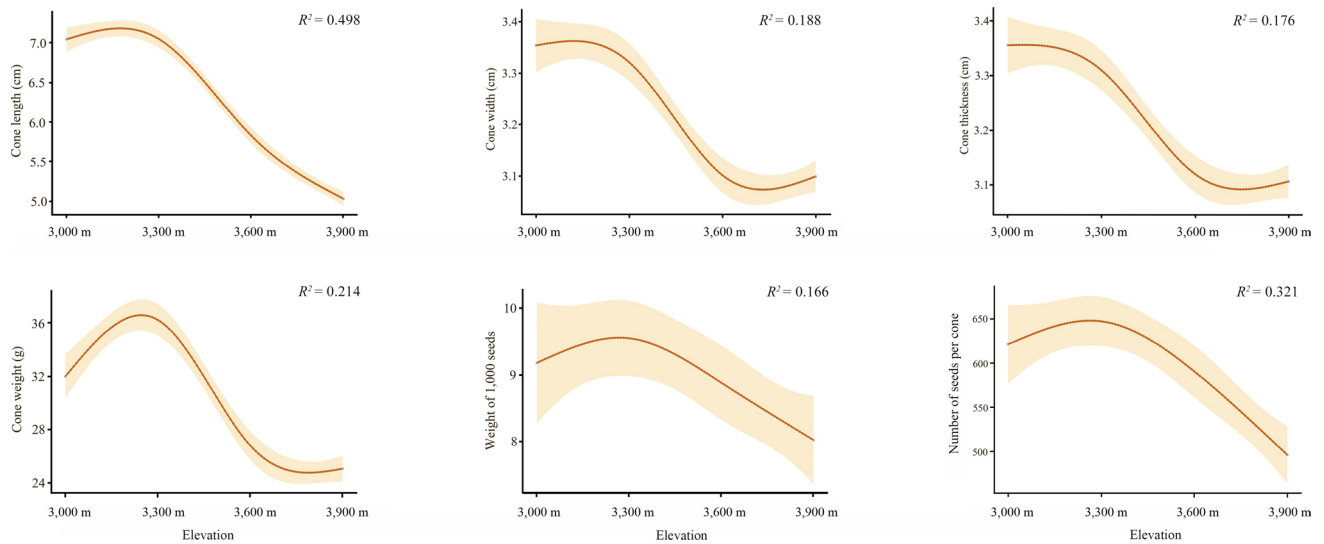


Fig. 5 Elevation adaptation of the Generalized Additive Model to cone traits. Note: The light brown band represents the 95% confidence interval range

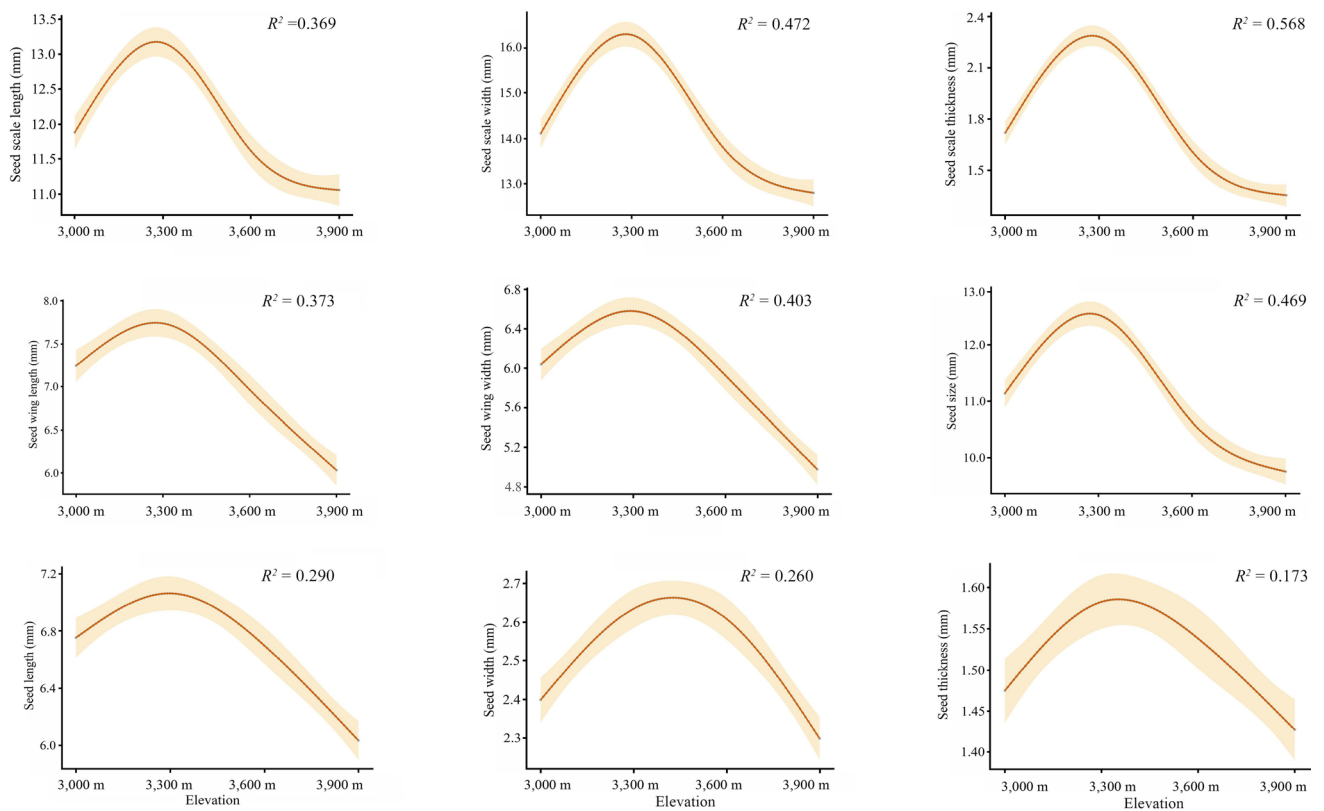


Fig. 6 Elevation adaptation of the generalized additive model to seed traits. Note: The light brown band represents the 95% confidence interval range

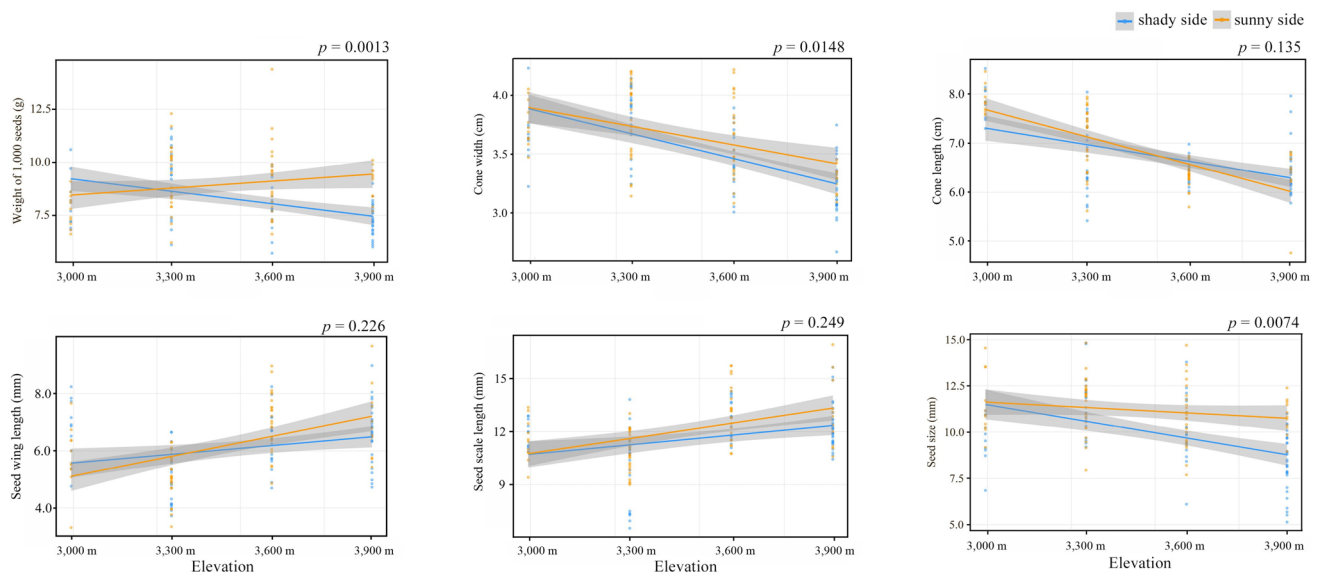


Fig. 7 Regulatory effects of crown direction on elevation response patterns of cone and seed traits

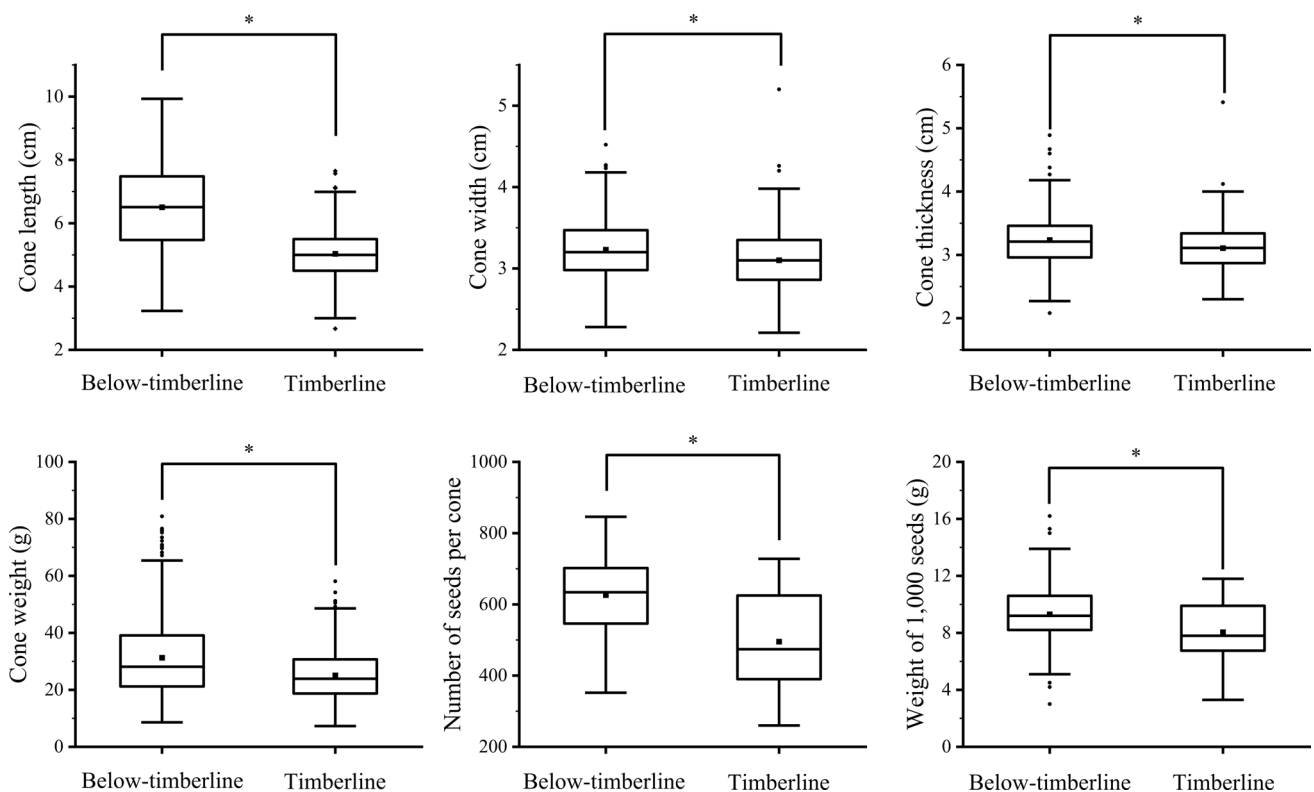


Fig. 8 Comparison of cone morphology traits between timberline and below-timberline areas. Note: Morphology traits refer to cone length, width, thickness, and weight; number of seeds per cone, and weight of 1,000 seeds. “*” represents a significant difference ($p < 0.05$)

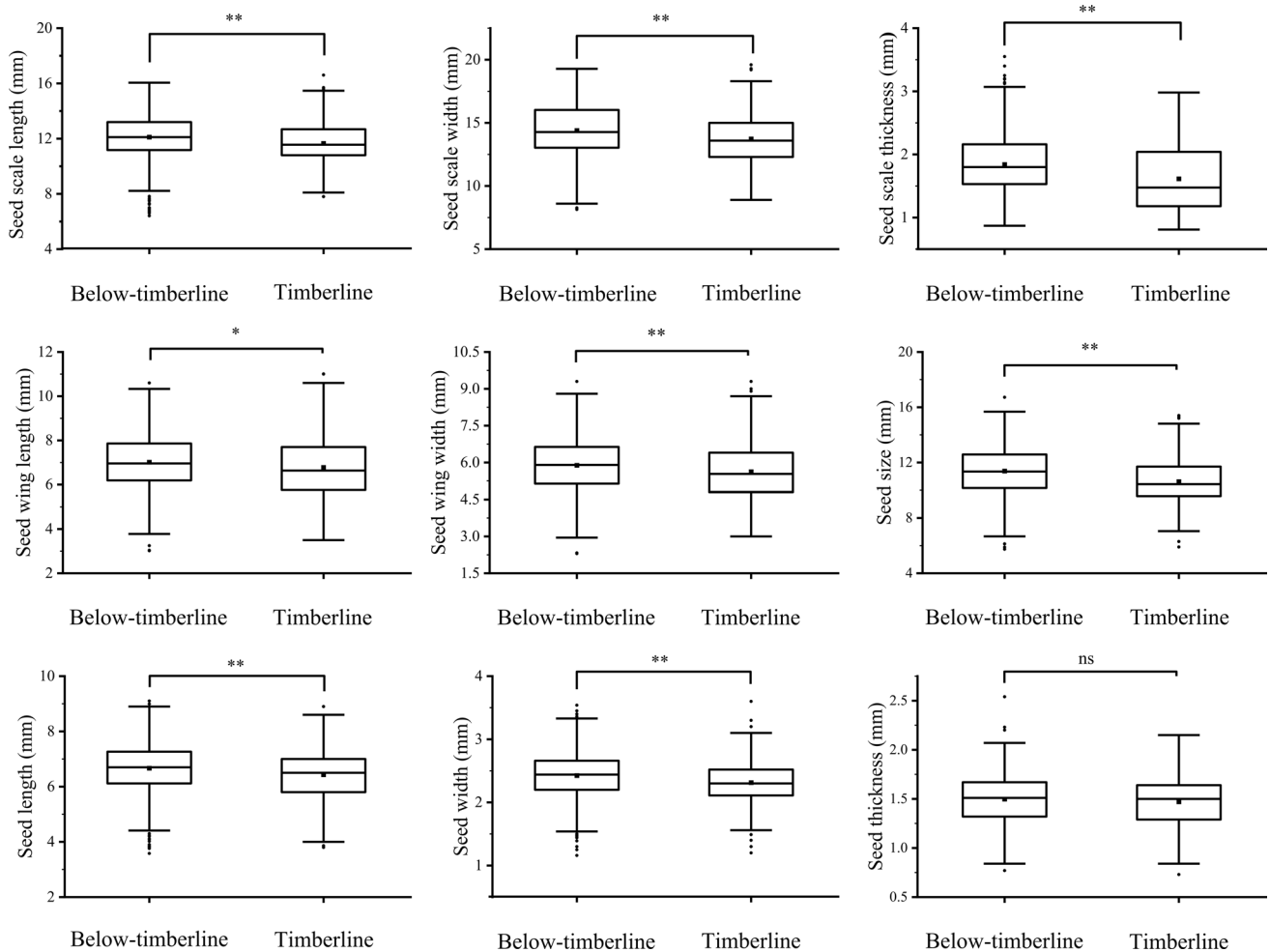


Fig. 9 Comparison of seed morphology traits between timberlines and other regions. Note: Morphology traits in Fig. 9 refer to seed length, width, thickness, size; seed scale length, width, thickness; seed wing length and width. “ns” represents no significant difference ($p > 0.05$) in this trait between timberline and below-timberline eco-

tones; “*” represents no significant difference ($p < 0.05$) in this trait between timberline and below-timberline ecotones; “**” represents a highly significant difference ($p < 0.01$) in this trait between timberline and below-timberline ecotones

Additionally, the CV for cone width and cone weight was highest at 3,300 m.

The trait diversity (TD) for CWD, CT, CW, 1000SW, SN, SWL, SWW, and SSW was highest at 3,900 m. In contrast, the TD for ST, SS, SL, SW, and SSL peaked at 3,600 m. Additionally, the TD for CT alone reached its maximum at 3,300 m. Overall, CV and TD of cone and seed traits were highest at high elevation (3,600–3,900 m), whereas traits at mid-elevation (3,300 m) showed the lowest variability and declining diversity (Table 2).

Discussion

Traits and germination characteristics of cones and seeds at different elevations

The morphological traits of Minjiang fir cones and seeds, such as seed length and cone length, exhibited a unimodal pattern along the elevation gradient, peaking at elevations of 3,300–3,600 m (Figs. 3 and 4). Habitat conditions and the physiological status of parent trees significantly

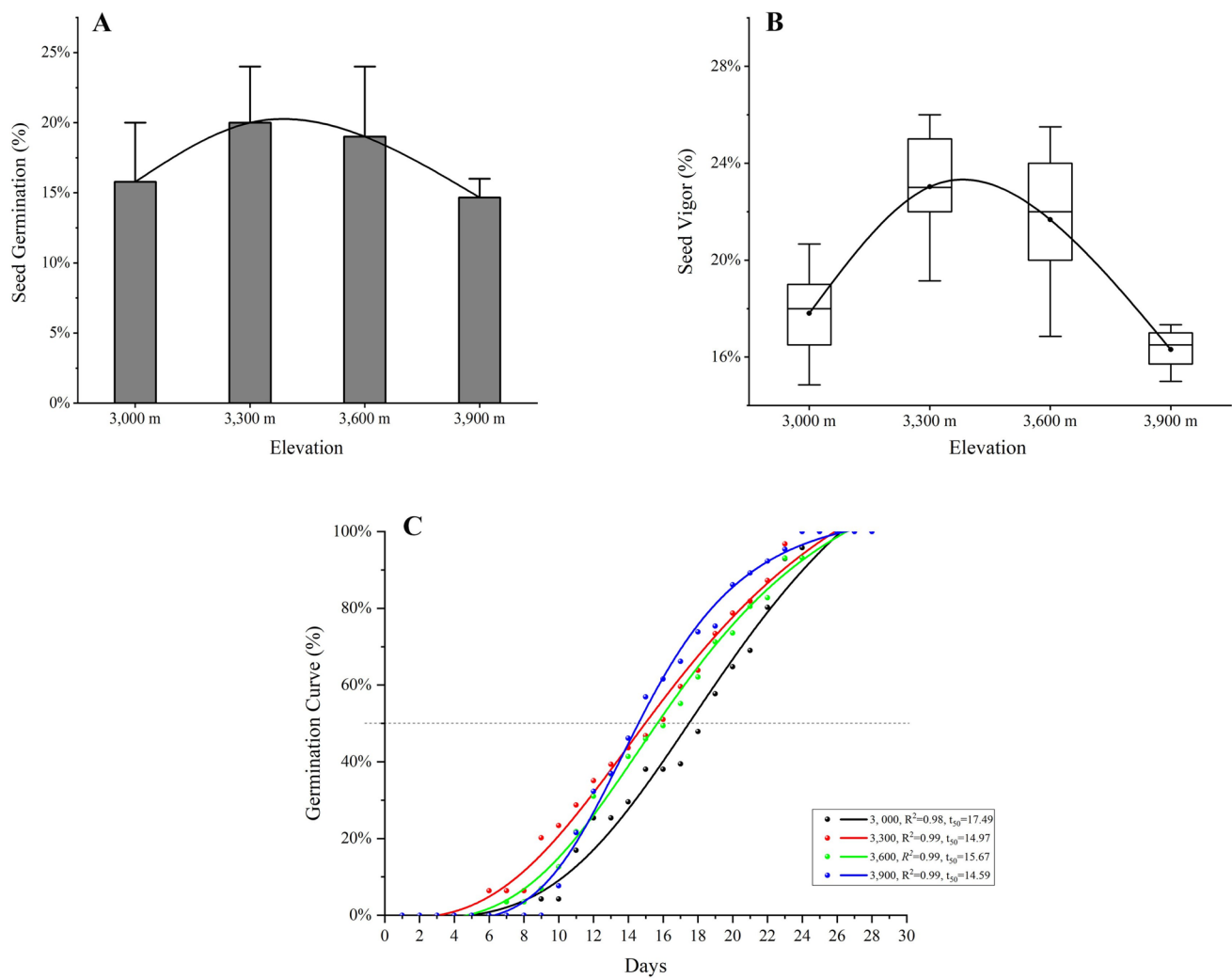


Fig. 10 Seed vigor **A**, seed germination rate **B**, and germination curve **C** with the increasing elevations. Note: t₅₀ indicates the number of days taken to reach a 50% cumulative germination rate

Table 2 Trait diversity and coefficient of variation in morphological traits of cones and seeds at different elevations (%)

Elevation		CL	CWD	CT	CW	1000SW	SN	ST	SST	SS	SWL	SWW	SL	SW	SSL	SSW
3,000	CV	0.156	0.099	0.096	0.343	0.158	0.113	0.136	0.260	0.150	0.166	0.173	0.145	0.163	0.147	0.145
	TD	1.661	1.792	1.758	1.631	1.723	1.607	1.828	1.948	1.793	1.815	1.890	1.892	1.882	1.862	1.882
3,300	CV	0.183	0.124	0.118	0.443	0.147	0.242	0.166	0.208	0.112	0.153	0.160	0.104	0.130	0.094	0.133
	TD	1.924	2.103	1.901	1.761	1.919	1.789	2.040	1.894	1.812	1.840	1.886	1.731	1.725	1.719	1.931
3,600	CV	0.196	0.107	0.120	0.374	0.185	0.285	0.195	0.210	0.190	0.186	0.189	0.175	0.172	0.167	0.150
	TD	1.848	1.934	1.872	1.729	2.034	1.774	2.146	1.622	2.109	1.98	2.036	2.145	1.926	2.079	1.981
3,900	CV	0.149	0.114	0.112	0.353	0.260	0.271	0.174	0.304	0.174	0.220	0.216	0.159	0.151	0.137	0.153
	TD	1.618	2.114	1.923	1.774	2.192	1.874	2.010	1.989	2.053	2.067	2.056	2.096	1.805	1.987	2.007

CL, cone length; CWD, cone width; CT, cone thickness; CW, cone weight; 1000SW, weight of 1,000 seeds; SN, number of seeds per cone; SSL, seed scale length; SSW, seed scale width; SST, seed scale thickness; SWL, seed wing length; SWW, seed wing width; SL, seed length; SW, seed width; ST, seed thickness; SS, seed size

influence cone and seed yield (Tang et al. 2001; Liu et al. 2011; Zou et al. 2008; Sun et al. 2005). In ecological research, similar hump-shaped patterns, where trait performance or community metrics peak at mid-elevations, have been extensively documented (Rahbek 2005; Körner 2003). Such patterns may be attributed to the fact that mid-elevation habitats provide the most suitable climatic conditions for growth and reproduction, where temperatures and resources are both adequate and neither becomes a major limiting factor. Seed mass, germination rate, and reproductive allocation often reach their highest values at moderate elevations, declining toward both lower and higher elevations (Olejniczak et al. 2018; Rosbakh et al. 2022). These observations indicate that mid-elevations represent ecologically suitable elevational ranges, where plants experience a balance between suitable growth conditions and tolerable levels of stress.

For Minjiang fir, the mid-elevation zone (3,300–3,600 m) may provide such a balance. Moderate temperatures, sufficient soil moisture, and relatively stable light conditions at these elevations are likely to promote effective carbon assimilation and nutrient accumulation, which in turn enhance reproductive allocation and cone development (Hagedorn et al. 2019; C. Wang et al. 2023a, b). In contrast, at higher elevations (> 3,600 m), environmental harshness intensifies—shorter growing seasons, low temperatures, freeze–thaw cycles, and nutrient-poor soils together constrain embryo formation and cone maturation. At lower elevations (< 3,000 m), dense understory vegetation (e.g., *Fargesia* spp.) and intensified competition for light and soil resources, combined with more substantial human disturbance, likely reduce not only seedling recruitment but also the resources available for cone maturation and seed filling. Studies have shown that above- and below-ground competition can significantly alter plant reproductive allocation and reproductive efficiency (Wang et al. 2014; Bonser 2013; Fazlioglu et al. 2016; Dostál et al. 2009), supporting the view that intense understory competition at comparatively low elevations may indirectly suppress reproductive investment in Minjiang fir.

Among climatic drivers, temperature plays the most decisive role in determining seed formation and maturation in alpine conifers. Studies on *Larix chinensis* near the Qinling Mountains timberline have revealed that seed and seed wing sizes decrease with increasing elevation, indicating adaptive responses to colder climates and stronger winds (Li et al. 2012; Wang et al. 2005). Smaller and lighter seeds at high elevations may represent an evolutionary adjustment to enhanced wind dispersal, favoring greater dispersal distance under strong updrafts. However, such adaptation often involves a trade-off between dispersal efficiency and seedling establishment potential, as smaller seeds generally contain fewer reserves for early growth. Therefore, the observed

decline in seed mass at high elevations likely reflects both physiological constraints and the habitat adaptation.

The unimodal pattern observed in Minjiang fir aligns with findings from other montane species. In *Larix chinensis*, seed production and the proportion of mature fruiting trees decline sharply with increasing elevation, reflecting reduced reproductive growth (Sun 2004; Wang et al. 2005). By contrast, *Polylepis australis* in Argentina showed no significant elevational effect on seed quality (Marcora et al. 2008), suggesting that the magnitude and direction of altitudinal responses can vary significantly among species and regions. Such interspecific variation underscores the importance of local adaptation: even within the same species, populations exposed to distinct microclimates may evolve different reproductive strategies to optimize fitness under their respective environmental regimes.

In the present study, the coefficient of variation (CV) for cone and seed traits was highest at 3,900 m, implying greater trait instability and stronger adaptive differentiation under extreme conditions. This variability may indicate that at high elevations, plants survive by modifying reproductive strategies, such as reducing seed size and uniformity, to cope with environmental unpredictability and physiological stress. Conversely, the mid-elevation populations (3,300–3,600 m) exhibited the lowest variability and the highest reproductive performance, including seed vigor (22%) and germination rate (20%). Such stability in both morphology and physiology suggests that these populations experience conditions that are relatively suitable for resource allocation and seed development.

In addition to climatic and physiological factors, the plasticity of reproductive resource allocation may further contribute to the mid-elevation peak. Plants dynamically adjust the balance between vegetative growth and reproduction in response to environmental pressures and energy availability (Scholl et al. 2020). Under moderately suitable conditions, such as those at mid-elevations, parent trees may allocate more resources toward reproductive organs, producing larger, more viable seeds. In contrast, in highly stressful or competitive environments, plants tend to prioritize maintenance and survival, resulting in smaller seeds and lower reproductive investment (Rosbakh et al. 2022; Fernández-Pérez et al. 2018). Moreover, field studies indicate that Minjiang fir populations can maintain relatively stable, growing population structures at suitable elevations (Wang et al. 2019). Elevational gradient studies on other alpine woody species have shown that mid-elevation stands often exhibit higher cone production and greater genetic diversity (Ju et al. 2022). Together with the well-established positive relationship between genetic diversity and population fitness (Reed and Frankham 2003), these patterns suggest that structurally stable, genetically diverse stands are likely to

achieve higher reproductive success and better seed quality through more effective pollen exchange and genetic mixing.

Overall, the unimodal pattern in cone and seed traits of Minjiang fir appears to result from the combined influences of climatic constraints and population-level adaptation. The mid-elevation belt (3,300–3,600 m) may therefore represent an ecologically suitable altitudinal range, where the interplay between temperature, moisture, and resource allocation is most conducive to reproductive success. This finding not only deepens our understanding of reproductive ecology in alpine conifers but also provides practical guidance for selecting high-quality seed sources to support the natural regeneration and restoration of subalpine fir forests on the eastern Qinghai-Tibet Plateau.

Seed traits in the below-timberline areas and timberline ecotones

The cones and seeds near the timberline ecotones exhibited declines in quantity and other morphological traits compared with those in below-timberline areas (Figs. 8 and 9). In typical small-seeded conifers, seed yield in forests to timberline ecotones can range from 0.1 to 10 million seeds/ha (Tranquillini 1979). However, seed quantity decreases dramatically near the timberline (Holtmeier and Broll 2020). Wardle (1970) reported that the yield and quality of *Nothofagus solandri* seeds in New Zealand declined near the timberline. Potential factors contributing to reduced seed quality near the timberline include sparse forest cover and smaller tree size in ecotone areas. Lower temperatures and soil nutrient levels in timberline areas significantly affect the productive capacity of tree seeds, including seed yield and quality (Körner and Paulsen 2004). Trees in timberline ecotone areas also experience longer intervals of mast years, reduced seed yield, and lower seed quality from their parent trees (Körner 2011). In this study, although Minjiang fir cones became smaller at the timberline, the decline in the number of seeds per cone slowed noticeably at high elevations, suggesting an adaptive response to extreme habitats.

In this study, the number of seeds per cone and the cone and seed quality were lower near the timberline than in below-timberline areas. Körner (2011) noted that seed size is among the most conserved traits and that trees tend to reduce seed size rather than seed quality under extreme conditions. Tranquillini (Tranquillini and Benecke, 1979) observed that *Abies alba* populations growing near the alpine timberline in the European Alps exhibited markedly reduced seed quality, characterized by a high proportion of empty or immature seeds, lower 1,000-seed weight, and decreased germination capacity. In a study by Holm (1994) on European white birch (*Betula pubescens*) in northern

Sweden, he observed a phenomenon of improved seed quality with increasing elevation.

Across alpine plants, seeds tend to germinate rapidly once suitable temperature and moisture conditions become available. This pattern represents an “accelerated germination strategy”, allowing seedlings to take advantage of the short frost-free period and reduce the risk of freezing damage during prolonged cold conditions (Wang et al. 2021; Fernández-Pascual et al. 2017; Vázquez-Ramírez and Venn 2021). Comparable patterns have been reported across multiple alpine or high-latitude species. For example, high-elevation populations of *Allium chrysanthum* on the eastern Qinghai-Tibet Plateau germinate significantly faster than their low-elevation counterparts once suitable temperatures are reached (Ge et al. 2020). Seeds of the relict tree *Euptelea pleiospermum* from higher elevations or latitudes also germinate earlier and show shorter t_{50} values under warm conditions (Wu et al. 2019). Similarly, high-latitude populations of *Asclepias syriaca* germinate earlier than those at lower latitudes when exposed to elevated temperatures (Mohl et al. 2023), and *Spartina alterniflora* populations from high latitudes exhibit strongly accelerated germination after cold stratification when subjected to warm temperatures (Cheng et al. 2022). In addition, research on dominant coniferous species in the subalpine timberline ecotone has found that alpine tree species at high elevations often adopt an r-strategy, producing a larger number of seeds to maximize regeneration success while reducing their seed quality (Shi 1999).

Performance in the morphological traits of seeds at different crown directions

Although crown direction has limited influence on seed quality and size in Minjiang fir, trees growing on shady slopes exhibited improved cone and seed traits on the sunny side of the crown (Supplementary Appendix 3 and 4). Tang et al. (2001) reported that the sunny side of parent trees produced more cones than the shady side, a finding consistent with our results. In *Pinus bungeana* populations of Hui County, Gansu, Wang (2002) found that crown direction had a marked influence on cone and seed development. Cones and seeds on the shady side exhibited significantly greater length, weight, and seed fullness, as well as higher weight of 1,000 seeds, compared with those on the sunny side. Crown direction significantly affected the morphology and size of cones and seeds. Seeds from the sunny side were larger and of higher quality than those from the shady side. This result is consistent with studies that cones and seeds on the sunny side develop more suitable traits due to greater exposure to light and heat (Xie et al. 1998; Lin and Liu 2008). Enhanced photosynthetic carbon fixation and carbohydrate allocation on the sunny side contribute to superior cone and seed traits

(Lin and Liu 2008). Although Minjiang fir is shade-tolerant, adequate light remains crucial for reproductive success, particularly for cone and seed development.

With increasing elevation, crown-direction effects became more pronounced, particularly for traits such as seed length, 1,000-seed weight, and cone width (Fig. 7). This is because thinner atmospheres at higher elevations amplify ultraviolet and solar radiation, widening the light and heat gap between sunny and shady sides. As a result, sunny-side branches allocate more resources to key reproductive traits, such as seed length, which directly affects endosperm reserves and early seedling establishment (Bian 2015). For successful regeneration, particularly in marginal or high-elevation habitats, prioritizing sunny-side seeds can substantially improve seedling competitiveness and survival.

Selection of seed sources and regeneration strategies

In this study, seed vigor and germination rate of Minjiang fir exhibited a pronounced hump-shaped pattern along the elevational gradient, with the highest values at 3,300 m (vigor was 22%; germination was 20%) and declining markedly at 3,900 m (vigor was 16%; germination was 15%). Seeds from high-elevation populations germinated earlier but achieved lower final germination rates, while seeds from low-elevation populations germinated more slowly. In contrast, mid-elevation populations (3,300–3,600 m) exhibited high vigor combined with moderate germination rates, reflecting an optimal balance between rapid germination and successful seedling establishment. This differentiation in germination behavior along elevation indicates that Minjiang fir populations adopt distinct regeneration strategies under different environmental constraints (Rosbakh et al. 2022). Seeds from high-elevation populations germinated earlier but achieved lower final germination rates, suggesting that under extremely harsh and cold conditions, seeds tend to germinate prematurely as a strategy to escape frost damage before winter (Liu and Zhang 2021). However, this accelerated germination is typically accompanied by smaller seed size and reduced energy reserves (Wang et al. 2021). Such an “accelerated germination–low reserve” pattern reflects a classic reproductive allocation model, in which plants sacrifice individual quality to ensure timely reproduction within a short growing season (Donohue et al. 2010; Moles and Westoby 2006).

Considering the morphological and germination traits, the mid-elevation (3,300–3,600 m) can be considered the priority altitudinal zone for seed sourcing. Seeds from this altitudinal zone exhibited larger, more developed seeds, higher vigor, and greater trait stability. Moderate temperatures and higher soil organic carbon and nitrogen contents at these elevations promote endosperm development and energy accumulation (Jia et al. 2022). In contrast, high-elevation

sites (> 3,900 m), characterized by frequent freezing events, nutrient-poor soils, and shortened reproductive periods (Körner 2011; Körner and Paulsen 2004), yielded comparatively smaller seeds with lower vigor, reflecting a constrained reproductive response under resource limitations. Altitudinal differentiation in reproductive traits of seeds has been reported for other coniferous species, such as *Abies bornmuelleriana* and *A. equi-trojani* in Turkey (Kurt et al. 2016), *Pinus pinaster* in Spain (Correia et al. 2014), and *Abies fraseri* in the U.S.A. (Emerson et al. 2008).

For seed collection and utilization, priority should be given to healthy, highly fertile parent trees located in mid-elevation regions. Given that the cones and seeds on the sunny side of the tree crown are usually larger and fuller, seed collection should prioritize the sunny side, which has higher temperatures and more abundant light, providing better conditions for cone and seed development (Kolotelo 1997). For other forestry workers, a comprehensive collection strategy involving multiple mother trees, different elevations and crown directions, and multi-year sampling will help maintain genetic diversity and adaptability. Additionally, we should protect high-elevation germplasm, as these materials may become potential cold-resistant genetic resource banks in the event of future climate warming (Alía et al. 2022; Breed et al. 2019).

Overall, the reproduction and regeneration of Minjiang fir are jointly regulated by elevation-related climatic drivers and species-specific patterns of resource allocation. The mid-elevation zone (3,300–3,600 m) represents an ecologically suitable altitudinal range for natural regeneration and should be considered a priority zone for seed sourcing in future conservation and restoration programs. Future research should focus on optimizing seed selection, breeding, and nursery propagation techniques by simulating the environmental conditions characteristic of this altitudinal window in controlled cultivation systems. Moreover, explicitly considering crown direction during seed sourcing—particularly collecting seeds from the sunny side, which exhibit superior morphology and vigor is expected to improve seedling quality, establishment, and early survival. Together, these efforts can form a robust technical and scientific foundation for cultivating *Abies* plantations and the long-term restoration of alpine coniferous forests.

Conclusions

On the eastern Qinghai-Tibet Plateau, the length and weight of Minjiang fir cones were 5.98 ± 1.36 cm and 29.06 ± 12.39 g. Seed size was 11.2 ± 1.9 mm; the weight of 1,000 seeds was 8.86 ± 2.31 g. The average seed vigor was 19.05%, while the laboratory germination rate was 17.61%. Seed scales were significantly larger than the seeds, and seed

wings were slightly longer or equal in length to the seeds, reflecting notable morphological differentiation. Cones also exhibited high variability in size and weight.

Cone and seed traits in the timberline ecotone performed markedly worse than those at mid-elevations. Most traits were optimal at 3,300–3,600 m, indicating that this elevation range represents the most suitable habitat for Minjiang fir reproduction. Seed vigor and germination rate also exhibited a unimodal distribution pattern, with vigor peaking at 22% at 3,300 m, decreasing to 16% at 3,900 m. Germination rate was 15.6% at 3,000 m, peaking at 20% at 3,300 m, and declining to 15% at 3,900 m, with data dispersion increasing slightly with elevation.

Phenotypic variation was evident between crown directions. Seeds on the sunny side were on average 2.45% larger than those on the shady side, with generally superior morphology, though differences in seed number per cone were not significant. Although the difference was insignificant, the overall morphology was superior on the sunny side. As elevation increased, the effects of different crown directions on the traits of Minjiang fir cones and seeds were not significantly different from each other, except for the cone width, the weight of 1,000 seeds, and seed size ($p < 0.05$).

Seed vigor and germination rate are positively correlated with cone length, cone weight, seed length, seed weight, tree height, diameter at breast height, and crown direction, and negatively correlated with elevation and the number of seeds per cone. Cone weight had the highest contribution to seed vigor and germination (21.5%), followed by elevation (18.39%). The evident elliptical clustering among the four elevations highlights that elevation is a key ecological driver of seed traits in Minjiang fir.

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