Effects of Temperature and Wind on the Growth and Physiology of *Pinus yunnanensis* var. *tenuifolia* Seedlings

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Abstract

Investigating the growth and physiological adaptability of offspring from Pinus yunnanensis var. tenuifolia populations to the high-temperature and strong-wind environments of their typical habitats is of great significance for understanding the adaptive evolution and developmental potential of this species. Pinus yunnanensis var. tenuifolia is one of the main tree species in the dry-hot valleys at the junction of Yunnan, Guizhou, and Guangxi in the upper reaches of the Pearl River, and is extremely important for maintaining soil and water conservation and vegetation ecology in this region. In this study, a seedling cultivation experiment was conducted using seeds from natural populations of Pinus yunnanensis var. tenuifolia in the Nanpanjiang-Hongshui River basin and seeds from natural populations of Pinus massoniana in the eastern neighboring region. Three treatments were established: 25℃ without wind (control), 30℃ without wind, and 25℃ with a wind speed of 1.2m・s-1, to simulate and explore the adaptive responses of seedling growth and physiology to high-temperature and wind environmental factors in the provenance areas. The results showed that: (1) Compared with Pinus massoniana, Pinus yunnanensis var. tenuifolia seedlings exhibited better growth and physiological performance under 30℃ and a wind speed of 1.2m・s-1, and the offspring of some Pinus yunnanensis var. tenuifolia populations were significantly superior to Pinus massoniana, indicating that Pinus yunnanensis var. tenuifolia is better adapted to dry-hot habitats. (2) Compared with the 25℃ environment, the ground diameter (+11.9%, $P < 0.05$) and average total root diameter (+9.41%, $P < 0.05$) of seedlings from various populations increased significantly under the 30℃ environment, while peroxidase activity decreased significantly (-68.1%, $P < 0.01$). Compared with the windless environment, the wind speed of 1.2m・s-1 significantly increased the average total root diameter (+11.1%, $P < 0.05$) and significantly decreased malondialdehyde content (-44.9%, $P < 0.05$). These results indicate that high-temperature and wind environments are conducive to the growth of Pinus yunnanensis var. tenuifolia seedlings, which adapt to dry-hot and windy environments by enhancing roots and stems while reducing stress-resistance responses. (3) Overall, antioxidant enzyme activities and peroxidation products were negatively correlated with annual mean temperature, monthly mean temperature, and wind speed, and positively correlated with elevation and annual precipitation, indicating that the growth and physiological adaptability of seedlings is mainly shaped by the coordinated selection of temperature, precipitation, wind, and elevation. In conclusion, the results of this study indicate that the dry-hot and strong-wind environment of the Nanpanjiang-Hongshui River valley is an important factor driving the development and evolution of Pinus yunnanensis var. tenuifolia.

Full Text

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Effects of Temperature and Wind on the Growth and Physiology of *Pinus yunnanensis* var. *tenuifolia* Seedlings

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Abstract: Exploring the growth and physiological adaptability of the offspring of *Pinus yunnanensis* var. *tenuifolia* populations to the high-temperature and strong-wind environments of their typical habitats is of great significance for understanding the adaptive evolution and developmental potential of this species. *Pinus yunnanensis* var. *tenuifolia* is one of the main arbor species in the dry-hot valley region at the junction of Yunnan, Guizhou, and Guangxi in the upper reaches of the Pearl River, and is extremely important for maintaining soil, water, and vegetation ecology in this region. In this study, nursery experiments were carried out using seeds from natural populations of *Pinus yunnanensis* var. *tenuifolia* in the Nanpanjiang-Hongshui River basin and seeds from natural populations of *Pinus massoniana* in the eastern adjacent area. Three treatments were established: 25 °C with no wind (control), 30 °C with no wind, and 25 °C with a wind speed of 1.2 $m \cdot s^{-1}$, to simulate and investigate the adaptive responses of seedling growth and physiology to the high-temperature and wind-exposure environmental factors of the provenance sites. The results showed that: (1) Compared with *P. massoniana*, seedlings of *P. yunnanensis* var. *tenuifolia* showed better growth and physiological performance under 30 °C and 1.2 $m \cdot s^{-1}$ wind speed, and the offspring of some *P. yunnanensis* var. *tenuifolia* populations were significantly superior to *P. massoniana*, indicating that *P. yunnanensis* var. *tenuifolia* is better adapted to hot habitats. (2) Compared with the 25 °C environment, under the 30 °C environment, seedling ground diameter (+11.9%, $P < 0.05$) and mean total-root diameter (+9.41%, $P < 0.05$) increased significantly, while peroxidase activity decreased significantly (−68.1%, $P < 0.01$). Compared with the windless environment, a wind speed of 1.2 $m \cdot s^{-1}$ significantly increased mean total-root diameter (+11.1%, $P < 0.05$) and significantly reduced malondialdehyde content (−44.9%, $P < 0.05$). This indicates that high-temperature and wind-exposure environments are beneficial to the growth of *P. yunnanensis* var. *tenuifolia* seedlings, enabling adaptation to hot and windy environments by strengthening roots and stems while reducing stress-resistance responses. (3) Overall, antioxidant enzyme activity and peroxidation products were negatively correlated with annual mean temperature, monthly mean temperature, and wind speed, and positively correlated with elevation and annual precipitation, indicating that the growth and physiological adaptability of the seedlings is mainly subject to the coordinated selection of temperature, precipitation, wind, and elevation. In summary, the results of this study indicate that the dry-hot and strong-wind environments of the Nanpanjiang–Hongshui River valley are important factors driving the development and evolution of *P. yunnanensis* var. *tenuifolia*.

Key words: ecological adaptability; seedling growth; resistance physiology; geographical environment; *Pinus yunnanensis* var. *tenuifolia*

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The influence of temperature and wind on the growth and physiology of *Pinus yunnanensis* var. *tenuifolia* seedlings

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Abstract: Exploring the growth and physiological adaptability of the offspring of wild *Pinus yunnanensis* var. *tenuifolia* (Pyt) populations to high temperatures and strong wind conditions in their typical habitats is crucial for understanding the adaptive evolution and developmental potential of this species. Pyt is one of the main tree species in the dry and hot valleys located at the junction of Yunnan, Guizhou, and Guangxi in the upper reaches of the Pearl River. It is very

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important to preserve the water, soil, and vegetation ecology in this area. This study conducted seedling cultivation experiments using wild populations of Pyt seeds collected from the Nanpan–Hongshui River Basin, along with one wild population of *P. massoniana* (Pm) from the adjacent eastern region. The 25 °C windless environment group was used as the control, while the 30 °C windless environment group and the 25 °C environment with a wind speed of 1.2 $m \cdot s^{-1}$ were established to investigate the adaptive responses of seedling growth and physiology to high temperature and wind conditions. The results demonstrated that: (1) Compared to Pm, Pyt seedlings exhibited superior growth and physiological performance under conditions of 30 °C and a wind speed of 1.2 $m \cdot s^{-1}$. Additionally, the offspring of certain Pyt populations performed significantly better than those of Pm. These findings demonstrate that Pyt possesses superior ecological suitability compared to Pm in dry-hot habitats. (2) The 30 °C environment induced significant increases in ground diameter (+11.9%, $P < 0.05$) and total root average diameter (+9.41%, $P < 0.05$), along with a marked reduction in peroxidase activity (−68.1%, $P < 0.01$) compared to 25 °C conditions. A wind speed of 1.2 $m \cdot s^{-1}$ significantly enhanced the average diameter of total roots (+11.1%, $P < 0.05$) and decreased malondialdehyde content (−44.9%, $P < 0.05$) relative to a windless environment, indicating that warm, windy conditions promoted phenotypic growth through reinforced root–stem development and reduced antioxidant demands. (3) Antioxidant enzyme activities and peroxidation product contents showed negative correlations with annual average temperature, monthly average temperature, and wind speed, but positive correlations with altitude and annual precipitation, indicating that the physiological adaptability of seedling growth is mainly influenced by the synergistic selections of temperature, precipitation, wind, and altitude. In summary, this study indicates that the dry, hot environment combined with strong winds in the Nanpan–Hongshui River valley is a critical factor driving the development and evolution of Pyt.

Keywords: ecological adaptability, seedling growth, resistance physiology, geographic environment, *Pinus yunnanensis* var. *tenuifolia*

Exploring the adaptive responses of forest trees to typical environmental factors in special habitats is of important guiding significance for understanding the adaptive evolution of forest trees and even the formation of species. The ecological adaptability of forest trees refers to the phenotypic and physiological traits that become adapted to the environment through changes in gene frequency and adjustments in genetic diversity under long-term environmental selection (Jia Cuirong, 2022). Seeds and seedlings are important carriers for the continuous reproduction and development of forest-tree populations and, to a certain extent, inherit the ecological adaptive characteristics of their parents. Therefore, investigating the relationship between seedling adaptability and environmental factors helps reveal the plastic potential of forest trees to adapt to changes in environmental factors (Booth, 2019; da Silva et al., 2022), which is crucial for the conservation of forest-tree resources under the background of climate change.

Plants can respond to changes in the external environment through a series of phenotypic traits (Chen et al., 2010; Teskey et al., 2015; Dong Yanping et al., 2023) and physiological traits (Cruz et al., 2019; Zhao Lijun et al., 2022; Li Qing et al., 2023). Measuring seedling growth indices and examining their growth performance under different environments is an important way to assess the adaptive potential of forest trees to climate change (Varsamis et al., 2019). Evaluation of the physiological and biochemical indices of seedlings under specific environments can, to a certain extent, elucidate the physiological adaptation mechanisms of forest trees to special habitats. Among them, malondialdehyde (MDA) content, peroxidase (POD), superoxide dismutase (SOD), catalase (CAT), polyphenol oxidase (PPO), and other indices are important indicators for measuring plant stress-resistance responses (Wei Qiumei et al., 2017). When facing single or combined stresses of drought and high temperature, these stress-resistance indices increase as temperature and drought severity intensify (Fu Zhiqiang et al., 2024; Tian Kaixin et al., 2024). However, in some plants that are originally adapted to dry-hot or wind stress, antioxidant enzyme activities do not change greatly under certain degrees of dry-hot or wind-blowing conditions (Li Li et al., 2014; Zhou Ruilian et al., 2021). Therefore, combining growth phenotypes with physiological and biochemical indices to explore the responses of early growth and development of forest trees to environmental factors

response mechanisms can provide important references for species conservation.

Fine-leaved Yunnan pine (*Pinus yunnanensis* var. *tenuifolia*) is a geographical variety of Yunnan pine (*P. yunnanensis*) that adapted eastward to the dry-hot valley terrain on the southeastern margin of the Yunnan–Guizhou Plateau. It is mainly distributed in the Nanpanjiang and Hongshui River basins, where it forms pure forests or conifer–broadleaf mixed forests along valleys. It is an important component of the ecological vegetation in the upper reaches of the Pearl River and is also a major afforestation tree species in northwestern Guangxi, with high ecological and economic value (Xu Xueliang, 1983). In recent years, the rapid expansion of planting areas of some economic tree species in this region, such as chestnut (*Castanea mollissima*), star anise (*Illicium verum*), and oil-tea camellia (*Camellia oleifera*), has severely fragmented the habitat of fine-leaved Yunnan pine and reduced its population size (Wu Dongshan et al., 2016). Relevant studies have shown that, although fine-leaved Yunnan pine still has relatively rich genetic diversity at the species level, habitat fragmentation has already exerted a non-negligible influence on gene flow among its populations (Yang Zhangqi et al., 2014; Liao et al., 2024). Research on the ecological adaptability and resource conservation of fine-leaved Yunnan pine is therefore particularly urgent. Although fine-leaved Yunnan pine is a narrowly distributed tree species, the environmental and climatic factors in its range are complex and variable. The special terrain of peak-cluster deep valleys, the resulting foehn effect, and the seasonal warm-dry climate may have driven adaptive responses in its seed-fruit phenotypes (Bai Tiandao et al., 2020), needle morphology (Feng Shanshan et al., 2023), and progeny genetic differentiation (Li et al., 2024; Liao et al., 2024). Liao et al. (2024) found that the landscape pattern of pollen flow among fine-leaved Yunnan pine populations is closely inseparable from the region' s distinctive peak-cluster terrain and foehn effect. The slender, drooping needles of fine-leaved Yunnan pine may also have been jointly shaped by the region' s seasonal warm-dry climate and canyon foehn winds (Feng Shanshan et al., 2023). Most of the above studies relied on field observations or indirect inference. Meanwhile, existing studies on fine-leaved Yunnan pine seedlings have focused on the effects of drought (Liu Yuanxin et al., 2023), growth hormones (Yi Hongtao et al., 2017), and light (Huang Zeyue et al., 2017) on seedlings. Although these studies have advanced our understanding of the adaptation of fine-leaved Yunnan pine to its special habitat, it remains unclear what growth-related and physiological–biochemical effects typical environmental factors of this habitat, such as temperature and wind, may have during seedling growth and development, and direct evidence under controlled conditions is lacking.

To reveal whether special environmental factors have a significant shaping effect on the growth, development, and adaptability of fine-leaved Yunnan pine seedlings, this study selected free-pollinated progeny seedlings from five natural populations of fine-leaved Yunnan pine on the basis of differences in wind speed, annual mean temperature, elevation, and geographical location. These populations provide good coverage of the narrowly distributed fine-leaved Yunnan pine populations. In addition, progeny from one natural population of Masson pine in the northeastern neighboring area, which has marked environmental differences and a close phylogenetic relationship (Huang Chunhui, 2023), was used as a control. The study mainly explored the effects of temperature and wind conditions on the growth and physiology of fine-leaved Yunnan pine seedlings. The specific questions addressed were as follows: (1) How do temperature and wind affect the growth and physiology of fine-leaved Yunnan pine and Masson pine seedlings? (2) Do different provenances of fine-leaved Yunnan pine differ in their responses to temperature and wind, and what are the underlying mechanisms? (3) Which provenance or provenances of seedlings show better adaptability? The results of this study are expected to provide important guidance for subsequent research on the adaptability of fine-leaved Yunnan pine and other forest resources in similar habitats, as well as for their conservation and utilization.

1 Materials and Methods

1.1 Experimental materials

According to survey and distribution records for fine-leaved Yunnan pine in the *Flora of China* and the literature (Li Zhiji et al., 1981; Xu Xueliang, 1983), cones were collected in mid-October 2021 from five fine-leaved Yunnan pine populations distributed along the Nanpanjiang–Hongshui River basin and from one natural Masson pine population in the eastern neighboring area (Table 1, Figure 1). In each population, 15 healthy adult individuals with straight trunks and relatively abundant fruiting were randomly selected as seed-bearing mother trees [diameter at breast height (DBH) > 20 cm]. The distance between mother trees was greater than 80 m. Using a pole pruner (20 m), 20–30 normally developed mature cones were collected from the middle and upper parts of the crown, placed in cloth bags, brought back to the laboratory, exposed to the sun to obtain seeds, and stored in a refrigerator at 4 °C.

Table 1. Location and meteorological factors of the sampled populations of *Pinus yunnanensis* var. *tenuifolia* and *P. massoniana*

Provenance	Provenance label	Longitude	Latitude	Altitude (m)	Slope degree (°)	Wind speed ($m \cdot s^{-1}$)	Annual mean temperature (°C)	Annual average relative humidity (%)	Annual precipitation (mm)
Baixi Tun, Tian'e County	BX	106°41′ E	25°06′ N	544.53	25~30	0.504	18.74	77.50	1 245.67
Jinzhongshan Township, Longlin County	JZS	104°89′ E	24°67′ N	1 060.56	30~35	1.556	17.99	79.59	1 238.66
Pingbang Village, Luodian County	PB	106°54′ E	25°24′ N	542.51	30~35	0.524	18.51	75.54	1 139.84
Qiaoma Town, Ceheng County	QM	105°59′ E	24°93′ N	1 060.9	30~35	0.970	17.14	79.27	1 253.27
Zhebao Township, Longlin County	ZB	105°36′ E	24°83′ N	799.48	35~40	1.132	18.59	79.46	1 235.09

Provenance	Provenance label	Longitude	Latitude	Altitude (m)	Slope degree (°)	Wind speed (m · s^{-1})	Annual mean temperature (°C)	Annual average relative humidity (%)	Annual precipitation (mm)
Zhemi Town, Pingtang County	ZM	107°18′ E	25°39′ N	745.92	15~20	1.224	16.46	75.42	1 231.21

Dots represent five natural populations of *Pinus yunnanensis* var. *tenuifolia*, and the triangle represents one natural population of *P. massoniana*. **BX.** Baixi Tun, Tian' e County; **JZS.** Jinzhongshan Township, Longlin County; **PB.** Pingbang Village, Luodian County; **QM.** Qiaoma Town, Ceheng County; **ZB.** Zhebao Township, Longlin County; **ZM.** Zhemi Town, Pingtang County. Same below. Population information is given in Table 1.

The round dots represent five natural populations of *P. yunnanensis* var. *tenuifolia*, while the triangle represents one natural population of *P. massoniana*. **BX**: Baixi Tun, Tian' e County; **JZS**: Jinzhongshan Township, Longlin County; **PB**: Pingbang Village, Luodian County; **QM**: Qiaoma Town, Ceheng County; **ZB**: Zhebao Township, Longlin County; **ZM**: Zhemi Town, Pingtang County. The same abbreviations are used below. Detailed population information is provided in Table 1.

Fig. 1 Geographic distribution of *Pinus yunnanensis* var. *tenuifolia* provenances

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1.2 Seedling cultivation

For each population, 200 seeds were randomly selected by family. After the seeds were thoroughly mixed by population, a fixed number of seeds was sampled using the quartering method, and full seeds were selected by flotation. A total of 720 seeds were sampled from each population. The seeds were soaked in clean water for 2 h, disinfected by soaking in 0.5% potassium permanganate solution for 20 min, rinsed three times with pure water, and sown in 72-cell seedling trays (upper opening diameter 40 mm, lower opening diameter 15 mm, depth 40 mm, volume 40 mL). The seedling substrate consisted of vermiculite (1/3) and nutrient soil (2/3), which was disinfected before use by placing it in an oven at 100 °C for 2 h. Six replicates were set for each provenance, with 120 seeds per replicate and four seeds per cell. After sowing, the seeds were covered with approximately 0.5 cm of substrate. After the substrate was thoroughly watered with clean water, the trays were placed in a constant-temperature, constant-humidity incubator (HWS-250B, Beijing Hengnuo Lixing Technology Co., Ltd.) for cultivation, with the temperature set to 25 °C, relative humidity to 75%, daily illumination to 12 h, and light intensity to 2 000 lx. Substrate moisture was measured daily using a handheld soil moisture meter (Xima Soil Detector PH-328); when moisture was insufficient, an appropriate amount of clean water was added. On the 25th day of each month, nutrient solution containing NPK ≥ 10 $g \cdot L^{-1}$; S, Mg, and Ca ≥ 1 $g \cdot L^{-1}$; and Fe, Mn, and Zn ≥ 0.2 $g \cdot L^{-1}$ was uniformly applied after dilution at 1:500, with 5 mL irrigated to supplement substrate nutrients. After 30 d, vigorous seedlings were selected and transplanted into seedling cups (upper diameter 7 cm, lower diameter 5 cm, height 7.5 cm) for subsequent experiments.

1.3 Experimental design

Existing studies generally consider temperature and foehn wind to be important factors shaping the adaptation of *Pinus yunnanensis* var. *tenuifolia* to its habitat (Li Chunye et al., 2016; Feng Shanshan et al., 2023). Based on data from the various provenance sites in this valley region, the maximum air temperature in the hottest month is 27–30 °C, and the mean wind speed is 0.5–1.55 $m \cdot s^{-1}$ (data from the WorldClim website: https://worldclim.org/data/worldclim21.html and the National Tibetan Plateau Data Center: https://data.tpdc.ac.cn/home). Although natural wind fluctuations such as instantaneous strong winds or changes in wind direction were considered, newly emerged seedlings are too delicate, and changing wind direction or increasing wind-speed intensity may cause a risk of seedling breakage. Therefore, in this experiment, single-factor, two-level tests were conducted for the two factors of temperature (25, 30 °C) and wind exposure (0, 1.2 $m \cdot s^{-1}$) (Table 2). Each treatment had three replicates, with 30 seedlings per replicate, and the treatment period was 90 d. For the wind-exposure condition, the incubator' s built-in constant-power fan at the bottom was used to operate continuously for 24 h; the outlet wind speed (1.2 $m \cdot s^{-1}$) was measured with a DEM6 digital portable three-cup wind-direction and wind-speed meter.

Table 2 Setting conditions for each treatment

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Treatment	Temperature	Wind speed	Air humidity (RH)	Cultivation time
Treatment	Temperature (°C)	Wind speed ($m \cdot s^{-1}$)	Air humidity (%)	Growing time (d)

Treatment	Temperature	Wind speed	Air humidity (RH)	Cultivation time
$120d_{25^\circ\mathrm{C}}$	25	0	75	120
$120d_{30^\circ\mathrm{C}}$	30	0	75	120
$120d_{25^\circ\mathrm{C}-1.2\,\mathrm{m\cdot s^{-1}}}$	25	1.2	75	120

1.4 Indicator measurement

Growth phenotypic indicators: For each population, 15 healthy seedlings aged 120 d with balanced growth were randomly selected. An analytical balance ($±$0.1 mg) was used to measure the fresh weight (FW) of each individual plant. The seedlings were then scanned (EU-88EPSON root measurement system, Japan) to obtain whole-plant images. WinRHIZO software (Pan Yanfei et al., 2024) was used to measure total root length (TRL), total root surface area (TRSA), total root projected area (TRPA), and average total root diameter (ADTR). ImageJ software (Schneider et al., 2012) was used to measure seedling height (SH) and basal diameter (BD).

Physiological and biochemical indicators: For each provenance, six healthy seedlings with balanced growth were randomly selected. From each plant, 0.2 g of needles was weighed, and ⋯

Add 2 mL of 0.05 $\mathrm{mol\cdot L^{-1}}$ phosphate buffer (pH = 7), 0.1 g polyvinylpyrrolidone (PVP), and a small amount of quartz sand; grind in a mortar in an ice bath to form a homogenate. Transfer it to a 10 mL centrifuge tube, rinse the mortar with 8 mL PBS solution, pour the rinse into the centrifuge tube, mix well, and centrifuge at 0–4 ℃ and 5 000 g for 20 min. The supernatant was collected as the enzyme extract, aliquoted, and stored in a −80 ℃ freezer. This enzyme extract was used for determination of antioxidant enzymes (SOD, POD, PPO, and CAT) and MDA content. MDA content was determined by the thiobarbituric acid method; SOD activity was determined by the nitroblue tetrazolium (NBT) colorimetric method; CAT activity was determined by ultraviolet absorption spectrophotometry (Liu Fengquan et al., 2001); POD activity was determined by the guaiacol method; and PPO activity was determined by the catechol method (Zhao Shiguang et al., 1993). For POD, CAT, and PPO, one enzyme activity unit (U) was defined as a change of 0.01 in OD per minute per gram fresh weight (FW), whereas for SOD, one enzyme activity unit was defined as 50% inhibition of NBT. Detailed information on each tested indicator is shown in Table 3.

Table 3 Names, abbreviations, and units of tested trait indicators for *Pinus yunnanensis* var. *tenuifolia* seedlings

Abbreviations of trait	Unit	Names of trait
FW	g	Fresh weight

Abbreviations of trait	Unit	Names of trait
BD	cm	Ground diameter
SH	cm	Seedling height
TRL	cm	Total root length
TRSA	cm^2	Total root surface area
TRPA	cm^2	Total root projected area
ADTR	mm	Average diameter of total roots
CAT	$U \cdot min^{-1} \cdot g^{-1}$ FW	Catalase
POD	$U \cdot min^{-1} \cdot g^{-1}$ FW	Peroxidase
SOD	$U \cdot g^{-1}$ FW	Superoxide dismutase
PPO	$U \cdot min^{-1} \cdot g^{-1}$ FW	Polyphenol oxidase
MDA	$\mu mol \cdot g^{-1}$ FW	Malondialdehyde

1.5 Data processing

R 4.4.0 software (R Core Team, 2024) was used to apply natural logarithmic transformation to non-normally distributed data among treatments and provenances. Linear regression models were fitted for analysis of variance, and marginal mean estimation and multiple comparisons of the linear models were performed using the Sidak method. Pearson correlation coefficients were used to test the correlations between each indicator and environmental factors at the provenance sites. Principal component analysis (Shang Fuqiang et al., 2024) and the membership function method (Zhang et al., 2024) were used to comprehensively evaluate the phenotypic and physiological indicators of *Pinus yunnanensis* var. *tenuifolia* seedlings from different provenances. The membership function values were calculated as follows:

$$U(X_{ij}) = (X_{ij} - X_{j\,\min})/(X_{j\,\max} - X_{j\,\min}) \quad (1)$$

$$U(X_{ij}) = 1 - (X_{ij} - X_{j\,\min})/(X_{j\,\max} - X_{j\,\min}) \quad (2)$$

where $U(X_{ij})$ is the membership function value of trait j for provenance i; X_{ij} is the measured value of trait j for provenance i; and $X_{j\,\min}$ and $X_{j\,\max}$ are the minimum and maximum values of trait j, respectively. When an indicator was positively correlated with the comprehensive evaluation result, formula (1) was used; when an indicator was negatively correlated with the comprehensive evaluation result, formula (2) was used.

2 Results and analysis

2.1 Effects of temperature and wind on the growth phenotype and antioxidant enzyme activities of *Pinus yunnanensis* var. *tenuifolia* seedlings

Analysis of variance showed that the main effect of the 30 ℃ environment had significant effects on ground diameter, average diameter of total roots, and POD activity of *Pinus yunnanensis* var. *tenuifolia* seedlings ($P < 0.05$); the main effect of the 1.2 $m \cdot s^{-1}$ wind-speed environment significantly affected average diameter of total roots, PPO activity, and MDA content ($P < 0.05$). Multiple-comparison analysis (Fig. 2) showed that, at 25 ℃ for 120 d, differences in growth phenotype among provenances of *Pinus yunnanensis* var. *tenuifolia* seedlings were not obvious, but treatments under 30 ℃ and 1.2 $m \cdot s^{-1}$ wind-speed conditions both promoted, to varying degrees, the fine-leaved

The growth traits (except seedling height) of *Pinus yunnanensis* var. *tenuifolia* seedlings differed in response among provenances, indicating that the environmental effects of high temperature and wind promoted phenotypic growth of the seedlings to a certain extent. Under 120 d at 30 °C, fresh weight and basal diameter differed significantly among provenances. Under 120 d with a wind speed of 1.2 m·s^-1, fresh weight, total root length, total root surface area, and total root projected area differed significantly among provenances. This may be attributable to differences in the responses of the provenances to environmental factors, or to differences in genetic diversity among provenances. Considering all growth phenotypic traits together, the growth indicators of QM (Qiaoma provenance) and JZS (Jinzhongshan provenance) were generally larger and showed more prominent growth phenotypes, whereas ZB (Zhebao provenance) was generally smaller.

Visible labels in Fig. 2. Panels: A, fresh weight (g); B, basal diameter (cm); C, total root surface area (cm^2); D, total root projected area (cm^2); E, total root length (cm). Provenances: BX, JZS, PB, QM, ZB, ZM. Treatments: 120d25°C, 120d30°C, and 120d25°C-1.2m·s^-1. Visible significance labels above bars include a, ab, and b. Visible probability labels include $P_{t30} = 0.0171$, $P_{t25w} = 0.0357$, $P_{t30} = 0.0189$, $P_{t25w} = 0.0078$, and $P_{t25w} = 0.008$.

P_{t25}. Variance analysis of provenances under the experimental condition of 120 d at 25 °C; P_{t30}. Variance analysis of provenances under the experimental condition of 120 d at 30 °C; P_{t25w}. Variance analysis of provenances under the experimental condition of 120 d at 25 °C with a wind speed of 1.2 m· s^-1. Different lowercase letters above the bars indicate significant differences among provenances under the same treatment ($P < 0.05$), while the same letters indicate no significant differences. The same below.

Fig. 2 Growth indicators of *Pinus yunnanensis* var. *tenuifolia* seedlings under different environments

Under 120 d at 25 °C, antioxidant enzyme activities (except SOD) and MDA content in *P. yunnanensis* var. *tenuifolia* seedlings differed significantly among provenances. Under the 30 °C environment, seedling POD, SOD, and MDA differed significantly among provenances. Under the 1.2 m · s^-1 environment, seedling POD, PPO, and MDA differed significantly among provenances. This indicates that the antioxidant capacities of different provenances responded differently to environmental factors, and may also reflect differences in genetic diversity among provenances. Different provenances showed different response patterns to high-temperature and wind environments (Fig. 3).

Among them, at 30 °C, POD activity decreased significantly in all provenances; MDA content showed the same pattern under the 1.2 $m \cdot s^{-1}$ wind-speed environment. This indicates that, under high-temperature and wind-blowing environments, the seedlings had a weak stress response and adapted to the environment; therefore, antioxidant enzyme activity and peroxidation-product content were low. Under the 1.2 $m \cdot s^{-1}$ wind-speed condition, the patterns of change in antioxidant enzyme activity and MDA content differed among provenances. Among them, the antioxidant enzyme activity and peroxidation-product content of the QM provenance decreased markedly, indicating that the QM provenance adapted significantly to the high-temperature and wind-blowing environment.

Fig. 3 Physiological indicators of *Pinus yunnanensis* var. *tenuifolia* seedlings under different environments

Figure panels:
A, catalase activity, CAT ($U \cdot min^{-1} \cdot g^{-1}$ FW), $P_{t25} = 0.0093$;
B, peroxidase activity, POD ($U \cdot min^{-1} \cdot g^{-1}$ FW), $P_{t25} = 0.0063$, $P_{t30} = 0.0042$, $P_{t25w} = 1.434 \times 10^{-8}$;
C, polyphenol oxidase activity, PPO ($U \cdot min^{-1} \cdot g^{-1}$ FW), $P_{t25} = 1.227 \times 10^{-6}$, $P_{t25w} = 0.0003$;
D, superoxide dismutase activity, SOD ($U \cdot g^{-1}$ FW), $P_{t30} = 5.139 \times 10^{-5}$;
E, malondialdehyde content, MDA ($mol \cdot g^{-1}$ FW), $P_{t25} = 2.843 \times 10^{-7}$, $P_{t30} = 0.0028$, $P_{t25w} = 1.098 \times 10^{-5}$.
Provenances: BX, JZS, PB, QM, ZB, ZM. Treatments: 120 d at 25 °C; 120 d at 30 °C; 120 d at 25 °C with 1.2 $m \cdot s^{-1}$ wind speed.

2.2 Analysis of Growth and Physiological Indicators of *Pinus yunnanensis* var. *tenuifolia* Seedlings and Environmental Factors

Principal component analysis was performed on the growth and physiological indicators under the two treatments. Under the 30 °C condition (Fig. 4: A, B), the cumulative contribution rate of the first two principal components reached 78.7%; principal component 1 (56.2%) had larger weighting coefficients for fresh weight, total root length, total root surface area, total root projected area, ground diameter, and SOD, while principal component 2 (22.5%) had larger weighting coefficients for MDA, POD, and total mean root diameter. Total mean root diameter was negatively correlated with MDA. Under the 1.2 $m \cdot s^{-1}$ wind-speed condition (Fig. 4: C, D), the cumulative contribution rate of the first two principal components reached 79.9%; principal component 1 (53.5%) had larger weighting coefficients for growth-phenotype indicators such as seedling height, fresh weight, and total root length, whereas principal component 2 (26.4%) had larger weighting coefficients for PPO, SOD, and total mean root diameter. Total mean root diameter was negatively correlated with PPO. This indicates that, under high-temperature and wind-blowing environments, principal component 1 and principal component 2 can be used as representatives of seedling growth phenotype and physiological traits, respectively, for provenance selection. Increases in growth phenotype have a positive promoting effect on seedling adaptation, while physiological indicators reflect the degree of stress-resistance response to stress factors. In addition, it can be seen that under the 1.2 $m \cdot s^{-1}$ wind-speed condition, the growth and physiological characteristics of seedlings from *Pinus massoniana* provenances and *Pinus yunnanensis* var. *tenuifolia* provenances gradually differentiated. Based on the principal component plots, QM and JZS were selected as two superior provenances.

Visible text in Fig. 4

- **A.** Scree plot of principal components. Y-axis: percentage of explained variance (%); X-axis: dimensions. Percentages for dimensions 1-10: 56.2%, 22.5%, 6.4%, 5.3%, 3.0%, 2.2%, 2.1%, 1.2%, 0.7%, 0.3%.
- **B.** PCA biplot. X-axis: principal component 1, Dim1 (56.2%); Y-axis: principal component 2, Dim2 (22.5%). Legend: Provenance—Baixitun, BX; Jinzhongshan Township, JZS; Pingbang Village, PB; Qiaoma Town, QM; Zhebao Township, ZB. Visible variable labels include ADTR, SOD, CAT, PPO, TRSA, TRPA, TRB, FW, SH, POD, MDA, and BD.
- **C.** Scree plot of principal components. Y-axis: percentage of explained variance (%); X-axis: dimensions. Percentages for dimensions 1-10: 53.5%, 26.4%, 11.5%, 2.7%, 2.5%, 1.3%, 0.8%, 0.7%, 0.4%, 0.1%.
- **D.** PCA biplot. X-axis: principal component 1, Dim1 (53.5%); Y-axis: principal component 2, Dim2 (26.4%). Legend: Provenance—Baixitun, BX; Jinzhongshan Township, JZS; Pingbang Village, PB; Qiaoma Town, QM; Zhebao Township, ZB. Visible variable labels include PPO, SOD, POD, MDA, SH, CAT, TRB, TRSA, TRPA, FW, BD, and ADTR.

A, B. Principal component analysis of growth and physiological indicators under the experimental condition $120d_{30^\circ\mathrm{C}}$; **C, D.** Principal component analysis of growth and physiological indicators under the experimental condition $120d_{25^\circ\mathrm{C}-1.2\,\mathrm{m\cdot s^{-1}}}$. Abbreviations of the tested trait indicators are shown in Table 3.

Fig. 4 Principal component analysis of growth and physiological indicators in high-temperature and windy environments

Correlation analysis showed that, under the 30 °C condition, the basal diameter and CAT, PPO, and SOD activities of fine-leaved Yunnan pine seedlings from different provenances were highly significantly negatively correlated with annual mean temperature ($P < 0.01$), whereas POD activity was highly significantly positively correlated with annual mean temperature. Mean total root diameter and POD activity were significantly negatively correlated with distance to rivers. CAT, PPO, and SOD activities were significantly positively correlated with elevation. PPO activity was significantly positively correlated with annual precipitation, precipitation of the wettest month, relative humidity, and wind speed, and was significantly negatively correlated with precipitation of the driest month and with longitude and latitude (Fig. 5: A, E). Under the wind-speed condition of $1.2\,\mathrm{m} \cdot \mathrm{s}^{-1}$, fresh weight, total root length, total root surface area, total root projected area, and CAT activity were significantly negatively correlated with annual mean temperature, whereas mean total root diameter was significantly positively correlated with the mean diurnal temperature range. POD and PPO activities were positively correlated with annual precipitation and precipitation of the wettest month. CAT and POD activities were significantly negatively correlated with precipitation of the driest month. CAT activity was significantly positively correlated with elevation. POD activity and MDA content were significantly positively correlated with distance to rivers. MDA content was highly significantly positively correlated with longitude and latitude, and significantly negatively correlated with relative humidity and wind speed (Fig. 5: B, E). Correlation analysis between monthly mean temperature and the growth and physiology of fine-leaved Yunnan pine seedlings showed that, under the 30 °C condition, basal diameter was significantly negatively correlated with the monthly mean temperatures in January, February, April–July, and October–December ($P < 0.05$) (Fig. 5: C). SOD activity was significantly negatively correlated with the monthly mean temperatures in July–October; CAT activity was significantly negatively correlated with the monthly mean temperatures in June–November; PPO activity was significantly negatively correlated with the monthly mean temperatures in February and April–December; and POD activity was significantly positively correlated with the monthly mean temperatures in January–May, November, and December (Fig. 5: F). Under the $1.2\,\mathrm{m} \cdot \mathrm{s}^{-1}$ wind-speed condition, total root length, total root surface area, and total root projected area were generally significantly negatively correlated with the monthly mean temperatures in January, February, April, May, and October–December (Fig. 5: D). MDA content was significantly negatively correlated with the monthly mean temperatures in January–May and December; except for March, CAT activity was significantly negatively correlated with the mean temperature of every month (Fig. 5: F).

A. Correlation analysis between growth indicators and environmental factors under the $120d_{30^\circ\mathrm{C}}$ experimental condition; **B.** correlation analysis between growth indicators and environmental factors under the $120d_{25^\circ\mathrm{C}-1.2\,\mathrm{m \cdot s^{-1}}}$ experimental condition; **C.** correlation analysis between growth indicators and monthly mean temperature under the $120d_{30^\circ\mathrm{C}}$ experimental condition; **D.** correlation analysis between growth indicators and monthly mean temperature under the $120d_{25^\circ\mathrm{C}-1.2\,\mathrm{m \cdot s^{-1}}}$ experimental condition; **E.** correlation analysis between physiological indicators and environmental factors under the $120d_{30^\circ\mathrm{C}}$

and $120d_{25^\circ C-1.2\,m\cdot s^{-1}}$ experimental conditions; **F.** correlation analysis between physiological indicators and monthly mean temperature under the $120d_{30^\circ C}$ and $120d_{25^\circ C-1.2\,m\cdot s^{-1}}$ experimental conditions. $*$ and $**$ indicate significant correlations at the 95% and 99% confidence levels, respectively. CAT.30, MDA.30, POD.30, PPO.30, SOD.30, and CAT.1.2, MDA.1.2, POD.1.2, PPO.1.2, SOD.1.2 indicate physiological indicators under the $120d_{30^\circ C}$ and $120d_{25^\circ C-1.2\,m\cdot s^{-1}}$ experimental conditions, respectively. temp01-12: monthly mean temperature from January to December. b01: annual mean temperature; b02: diurnal temperature range; b12: annual precipitation; b13: precipitation of the wettest month; b14: precipitation of the driest month; ele: elevation; long: longitude; lat: latitude; D: distance from river; MRH: relative humidity; Wind: wind speed. Abbreviations of the tested trait indicators are as shown in Table 3.

A. Correlation analysis between growth indicators and environmental factors under the experimental condition of 120 days at 30°C; **B.** Correlation analysis between growth indicators and environmental factors under the experimental condition of 120 days at 25°C with a wind speed of $1.2\,m\cdot s^{-1}$; **C.** Correlation analysis between growth indicators and monthly average temperature under the experimental condition of 120 days at 30°C; **D.** Correlation analysis between growth indicators and monthly average temperature under the experimental condition of 120 days at 25°C with a wind speed of $1.2\,m\cdot s^{-1}$; **E.** Correlation analysis between physiological indicators and environmental factors under the experimental conditions of 120 days at 30°C and 120 days at 25°C with a wind speed of $1.2\,m\cdot s^{-1}$; **F.** Correlation analysis between physiological indicators and monthly average temperature

under the experimental conditions of 120 days at 30°C and 120 days at 25°C with a wind speed of 1.2 m·s^-1. *, **indicate significant correlations at the 95% and 99% confidence levels, respectively. CAT.30, MDA.30, POD.30, PPO.30, SOD.30 and CAT.1.2, MDA.1.2, POD.1.2, PPO.1.2, SOD.1.2 indicate physiological indicators measured under the experimental conditions of 120 days at 30°C and 120 days at 25°C with a wind speed of 1.2 m·s^-1, respectively.** temp01-12. **The monthly average temperature from January to December;** b01. **Annual mean temperature;** b02. **Mean diurnal range;** b12. **Annual precipitation;** b13. **Precipitation of wettest month;** b14. **Precipitation of driest month;** ele. **Elevation;** long. **Longitude;** lat. **Latitude;** D. **Distance to river;** MRH. **Relative humidity;** Wind.** Wind speed. The abbreviations of the tested trait indicators are shown in Table 3.

Fig. 5 Pearson correlation between growth and physiological trait indicators of *Pinus yunnanensis* var. *tenuifolia* and geoclimatic factors

2.3 Analysis of membership function values of seedlings from different provenances under high-temperature and wind-blowing environments

Through comprehensive analysis and evaluation by the membership function method, differences were found in the membership function values of growth and physiological indicators related to stress resistance among seedlings of *Pinus yunnanensis* var. *tenuifolia* from different provenances. The ranking of the membership function values of the five tested provenances under the 30°C condition was QM > PB > BX > JZS > ZB, and under the 1.2 m • s^-1 wind-speed condition the ranking was QM > JZS > BX > PB > ZB.

Table 4 Membership function values of growth and physiological indicators of *Pinus yunnanensis* var. *tenuifolia* seedlings under 30°C and 1.2 m • s^-1 wind

Indicator category	Indicator	BX	JZS	PB	QM	ZB
Growth indicator	FW	0.361/0.283	0.432/0.406	0.443/0.318	0.689/0.518	0.365/0.105
Growth indicator	SH	0.555/0.435	0.232/0.496	0.352/0.478	0.305/0.608	0.243/0.275
Growth indicator	BD	0.384/0.863	0.470/0.677	0.450/0.566	0.785/0.635	0.264/0.402
Growth indicator	TRL	0.382/0.223	0.477/0.224	0.381/0.246	0.635/0.486	0.212/0.033
Growth indicator	TRSA	0.368/0.188	0.486/0.255	0.345/0.248	0.601/0.462	0.176/0.035
Growth indicator	TRPA	0.368/0.188	0.486/0.255	0.345/0.248	0.601/0.462	0.176/0.035
Growth indicator	ADTR	0.620/0.159	0.709/0.654	0.397/0.470	0.508/0.427	0.397/0.503
Growth indicator	Average	0.434/0.334	0.470/0.424	0.388/0.368	0.589/0.514	0.262/0.198
Physiological indicator	CAT	0.626/0.634	0.540/0.665	0.742/0.722	0.426/0.043	0.824/0.848

Indicator category	Indicator	BX	JZS	PB	QM	ZB
Physiological indicator	MDA	0.745/0.829	0.976/0.980	0.877/0.507	0.834/0.666	0.555/0.839
Physiological indicator	POD	0.668/0.935	0.746/0.951	0.801/0.815	0.790/0.872	0.619/0.571
Physiological indicator	PPO	0.774/0.689	0.638/0.851	0.767/0.786	0.530/0.750	0.660/0.568
Physiological indicator	SOD	0.592/0.515	0.280/0.331	0.682/0.576	0.330/0.550	0.924/0.378
Physiological indicator	Average	0.681/0.721	0.636/0.756	0.774/0.681	0.582/0.576	0.716/0.640
Total average	Total average	0.558/0.527	0.553/0.590	0.581/0.524	0.586/0.545	0.489/0.419

3 Discussion

3.1 Effects of temperature on seedling growth and physiology and their adaptive mechanisms

Compared with the 25°C condition, seedlings of *Pinus yunnanensis* var. *tenuifolia* from all provenances at 30°C showed significant increases in ground diameter (+11.9%, $P < 0.01$) and mean total root diameter (+9.41%, $P < 0.05$), while POD activity decreased significantly (-68.1%, $P < 0.001$), indicating

Under this temperature condition, phenotypic growth of seedlings was favored and the stress response was weakened. Principal component analysis showed that mean total root diameter was significantly negatively correlated with MDA content; this response pattern reveals the adaptive strategy of fine-leaved Yunnan pine to the high-temperature conditions of its native habitat.

Correlation analysis showed that, in a 30 °C environment, provenances originating from areas with higher annual mean temperature and monthly mean temperature had smaller ground diameter. This adaptive mechanism may involve two levels. (1) Long-term high-temperature selection pressure has genetically fixed heat-tolerant traits in fine-leaved Yunnan pine populations, resulting in a relatively high optimum growth temperature (Feng Yun et al., 2024; Yang Xiaojuan et al., 2024). (2) Under high-temperature environments, root systems develop preferentially, compensating for transpiration water loss caused by high temperature by enhancing absorption and transport capacity (Luo et al., 2020; Fonseca de Lima et al., 2021). This phenomenon reflects a conservative adaptive strategy of plants under extreme environments: under resource-limited conditions, survival is prioritized rather than rapid growth. Provenances farther from rivers, where precipitation is abundant, had smaller mean total root diameter; it is inferred that seedlings from these provenances tend toward rapid growth, resulting in relatively underdeveloped root systems (Wright et al., 1999; Santiago et al., 2007; Poorter et al., 2012). Overall, provenances from areas with high annual mean temperature, high monthly mean temperature, high longitude and latitude, low elevation, low annual precipitation, and low relative humidity enhance root-system and ground-diameter development, thereby improving absorption and transport efficiency to cope with hot–dry habitats, while exhibiting weak stress-resistance responses. This further supports the hypothesis that "high-temperature adaptation reduces stress response" : when environmental conditions approach the ecological optimum of a species, the activation level of its stress-resistance system decreases, allowing more resources to be allocated to growth and development. Literature based on genotype–environment association analysis also indirectly supports this conclusion (Huang Chunhui, 2023). The differentiated phenotypic and physiological adaptation of different provenances to the environment may be caused by gene-flow isolation resulting from complex topography and habitat fragmentation, which has increased genetic differentiation among provenances (Li et al., 2024; Liao et al., 2024).

3.2 Effects of Wind on Seedling Growth and Physiology and Their Adaptive Mechanisms

Compared with the windless environment, fine-leaved Yunnan pine seedlings under a wind speed of 1.2 $m \cdot s^{-1}$ showed a significant increase in mean total root diameter (+11.1%, $P < 0.05$), while MDA content decreased significantly (−44.9%, $P < 0.001$). The principal component analysis results were similar, indicating that fine-leaved Yunnan pine seedlings are better adapted to windy environments; under windy conditions, their stability and root absorption and transport capacity are stronger, and their stress-resistance response is lower. Pearson correlation analysis showed that provenances from environments with high wind speed, high temperature, low precipitation, and low elevation had better root growth and lower stress-resistance responses. This phenomenon indicates that the shaping effect of wind environments on seedlings is mainly manifested in two aspects. Morphologically, the wind environment intensifies water loss, and its continuous mechanical stimulation induces root thickening, enhancing plant stability and absorption–transport capacity and meeting the demands of transpiration and cellular osmotic regulation (Bassirirad, 2000; Luo et al., 2020). Physiologically, the decreases in antioxidant enzyme activity and MDA content indicate that fine-leaved Yunnan pine has evolved an efficient antioxidant defense system to cope with oxidative pressure caused by wind stress. Meanwhile, the correlation analysis results support the conclusion that natural regeneration of fine-leaved Yunnan pine populations in low-mountain areas is relatively good (Zheng Dangbin et al., 2022). The differentiated responses of different provenances to wind environments reflect the existence of local adaptation. Provenances from high-wind-speed environments exhibited stronger wind adaptability. Phenotypic differentiation among provenances may be the result of the combined effects of restricted gene flow (Yang Zhangqi et al., 2014; Liao et al., 2024) and local selection pressure. In particular, within the complex canyon terrain of this region, wind-field characteristics differ markedly among locations, providing selective impetus for local adaptation of populations.

3.3 Comparison with Masson Pine and Selection of Superior Provenances

Compared with Masson pine, fine-leaved Yunnan pine seedlings in all environments had greater fresh weight, ground diameter, total root length, total root surface area, total root projected area, and other indicators, and lower stress-resistance responses. In other words, the growth performance and stress-resistance response of fine-leaved Yunnan pine under high-temperature and windy environments were both superior to those of Masson pine. This difference stems from differences in the survival environments of the two species. Fine-leaved Yunnan pine has long been adapted to hot-valley environments, and its phenotypic and physiological metabolic systems have been optimized to adapt to the combined effects of high temperature and wind stress (Li Zhiji et al., 1981; Wang Xianpu, 1991). By contrast, Masson pine, as a representative tree species of subtropical humid environments, has physiological mechanisms better suited to mild and humid conditions (Zhou Yufei et al., 2025).

Studying the growth and physiological traits of different provenances of fine-leaved Yunnan pine under the same environment can, to a certain extent, reflect seedling adaptability and stress resistance to the environment. This has important reference value for screening superior provenances during artificial vegetation restoration. Although this paper only discusses the independent effects of temperature and wind on the growth adaptability of fine-leaved Yunnan pine seedlings and does not address their interaction, the results of this paper allow a reasonable inference that the superposition of appropriately high temperature and windy conditions may be more suitable for the growth of fine-leaved Yunnan pine seedlings. Principal component analysis and membership function analysis showed that the provenances from Qiaoma Town, Ceheng County (QM), and Jinzhongshan Township, Longlin County (JZS), performed prominently in growth traits and stress adaptation, and were relatively well adapted to high-temperature and windy environments. The superior performance of these two provenances may be related to the environmental characteristics of their provenance sites: moderate environmental stress both promoted the evolution of stress-resistance traits and had not yet reached the extreme···

extremity. This finding has important guiding significance for the conservation and utilization of *Pinus yunnanensis* var. *tenuifolia*. In silvicultural planting and ecological restoration, priority should be given to provenances that have both good growth potential and strong environmental adaptability.

4 Conclusions and Outlook

This study shows that appropriate high-temperature and wind-exposure environments are favorable for the phenotypic growth of *Pinus yunnanensis* var. *tenuifolia* seedlings, which exhibit relatively low stress responses. Their growth and physiological performance are superior to those of the offspring of *Pinus massoniana* from neighboring (non-dry-hot) habitats. The offspring of *P. yunnanensis* var. *tenuifolia* populations located in areas with higher annual (monthly) mean temperatures, higher wind speeds, and lower elevations showed increased biomass and root systems, and stronger adaptability to high-temperature and wind-exposure environments. This indicates that populations from special habitats have acquired ecological advantages favorable for survival in such environments through long-term selection and adaptive evolution, and that these advantages are genetically transmitted to offspring, thereby sustaining population reproduction. At the same time, their special phenotypic and physiological responses have developed a certain degree of dependence on, and requirement for, particular environmental factors; once removed from that environment, their growth and physiological performance decline.

Although this study, based on controlled experiments, reveals to a certain extent the adaptive characteristics of *P. yunnanensis* var. *tenuifolia* offspring to factors in their native habitat, the seedling cultivation and testing period was relatively short. Future work could extend the testing period and add interactive, superimposed environmental factors and gradients, so as to obtain more robust results and provide a reference for the ecological conservation of *P. yunnanensis* var. *tenuifolia*.

References:

BAI TD, YU CL, GAN ZC, et al., 2020. Association of cone and seed traits of *Pinus yunnanensis* var. *tenuifolia* with geo-meteorological factors [J]. Chinese Journal of Plant Ecology, 44(12): 1224–1235. [Bai Tiandao, Yu Chunlan, Gan Zechao, et al., 2020. Association between variation in cone and seed traits of *Pinus yunnanensis* var. *tenuifolia* and geo-meteorological factors [J]. Chinese Journal of Plant Ecology, 44(12): 1224–1235.]

BASSIRIRAD H, 2000. Kinetics of nutrient uptake by roots: responses to global change [J]. New Phytologist, 147(1): 155–169.

BOOTH TH, 2019. Assessing the thermal adaptability of tree provenances: an example using *Eucalyptus tereticornis* [J]. Australian Forestry, 82(4): 176–180.

CHEN P, WELSH C, HAMANN A, 2010. Geographic variation in growth response of Douglas-fir to interannual climate variability and projected climate change [J]. Global Change Biology, 16(12): 3374–3385.

CRUZ MV, MORI GM, SIGNORI-MÜLLER C, et al., 2019. Local adaptation of a dominant coastal tree to freshwater availability and solar radiation suggested by genomic and ecophysiological approaches [J]. Scientific Reports, 9(1): 19936.

DONG YP, WANG B, WEI YL, et al., 2023. Leaf micromorphological, photosynthetic physiological characteristics and their ecological adaptability of dominant tree species in a karst seasonal rain forest in Guangxi, China [J]. Guihaia, 43(3): 415–428. [Dong Yanping, Wang Bin, Wei Yulian, et al., 2023. Leaf micromorphological and photosynthetic physiological characteristics of dominant tree species in a karst seasonal rain forest and their ecological adaptability [J]. Guihaia, 43(3): 415–428.]

DA SILVA PHM, ARAUJO MJ, LEE DJ, et al., 2022. Adaptability and stability of novel *Eucalypt* species and provenances across environments in Brazil at two assessment [J]. New Forests, 53(5): 779–796.

FENG SS, HUANG CH, TANG MY, et al., 2023. Geographical variation of needles phenotypic and anatomic traits between populations of *Pinus yunnanensis* var. *tenuifolia* and its environmental interpretation [J]. Chinese Journal of Plant Ecology, 47(8): 1116–1130. [Feng Shanshan, Huang Chunhui, Tang Mengyun, et al., 2023. Geographic variation in needle morphology and microanatomical traits of *Pinus yunnanensis* var. *tenuifolia* and its environmental interpretation [J]. Chinese Journal of Plant Ecology, 47(8): 1116–1130.]

FENG Y, ZHANG Y, FAN SH, et al., 2024. Leaf phenotypic variations of the 12 bamboo species and their relationships with environmental factors [J]. Journal of Northwest Forestry University,

39(1): 147-153. [FENG Yun, ZHANG [[unclear: given name]], FAN Shaohui, et al., 2024. Leaf phenotypic variation in 12 bamboo species and its relationship with environmental factors [J]. Journal of Northwest Forestry University, 39(1): 147-153.]

FU ZQ, ZHANG H, LIU Z, et al., 2024. Evaluation of the physiological response and heat tolerance of seedlings of different *Camellia oleifera* cultivars to high temperature stress [J]. Forest Research, 37(2): 189–200. [FU Zhiqiang, ZHANG Heng, LIU Zhen, et al., 2024. Physiological responses and heat-tolerance evaluation of seedlings of different oil-tea camellia cultivars under high-temperature stress [J]. Forest Research, 37(2): 189-200.]

FONSECA DE LIMA CF, KLEINE-VEHN J, DE SMET I, et al., 2021. Getting to the root of belowground high temperature responses in plants [J]. Journal of Experimental Botany, 72(21): 7404–7413.

HUANG CH, 2023. Molecular phylogeography of *Pinus yunnanensis* var. *tenuifolia* [D]. Nanning: Guangxi University. [HUANG Chunhui, 2023. Phylogeographic study of the molecular systematics of *Pinus yunnanensis* var. *tenuifolia* [D]. Nanning: Guangxi University.]

HUANG ZY, ZENG QJ, ZHAO YH, et al., 2017. Physiological responses of *Pi-*

nus yunnanensis var. *tenuifolia* seedlings to different light intensities [J]. Journal of Henan Agricultural Sciences, 46(6): 108-112. [HUANG Zeyue, ZENG Qingjian, ZHAO Yihui, et al., 2017. Physiological responses of *Pinus yunnanensis* var. *tenuifolia* seedlings under different light conditions [J]. Journal of Henan Agricultural Sciences, 46(6): 108-112.]

JIA CR, 2022. Selecting proper restriction enzymes for genotyping-by-sequencing library construction and local adaptation to climate in *Eucalyptus grandis* [D]. Beijing: Chinese Academy of Forestry. [JIA Cuirong, 2022. Optimization of restriction endonucleases for GBS library construction and its application in the analysis of climate adaptation in *Eucalyptus grandis* [D]. Beijing: Chinese Academy of Forestry.]

LI CY, WANG YB, LIAO CY, et al., 2016. Research progress of *Pinus yunnanensis* var. *tenuifolia* [J]. Forest Inventory and Planning, 41(6): 30-34. [LI Chunye, WANG Youbing, LIAO Congning, et al., 2016. Research progress on *Pinus yunnanensis* var. *tenuifolia* [J]. Forest Inventory and Planning, 41(6): 30-34.]

LI L, LIU YM, WANG M, et al., 2014. Physiological response mechanism of three kinds of *Acer rubrum* L. under continuous high temperature and drought stress [J]. Acta Ecologica Sinica, 34(22): 6471-6480. [LI Li, LIU Yumin, WANG Min, et al., 2014. Physiological response mechanisms of three kinds of North American red maple under continuous high-temperature and drought stress [J]. Acta Ecologica Sinica, 34(22): 6471-6480.]

LI Q, YAO Y, HE YT, et al., 2023. The ecological adaptability of dominant poplar species to alpine environments in the Yarlung Zangbo River Basin [J]. Journal of Sichuan University (Natural Science Edition), 60(5): 203-211. [LI Qing, YAO Yuan, HE Yutong, et al., 2023. Ecological adaptability of dominant poplar plantation species to alpine environments in the Yarlung Zangbo River Basin [J]. Journal of Sichuan University (Natural Science Edition), 60(5): 203-211.]

LI ZJ, WANG XB, 1981. The distribution of *Pinus yunnanensis* var. *tenuifolia* in relation to the environmental conditions [J]. Plant Ecology and Phytogeography Series, 5(1): 28-37. [LI Zhiji, WANG Xianpu, 1981. The geographical distribution of *Pinus yunnanensis* var. *tenuifolia* in Guangxi and its relationship with the environment [J]. Plant Ecology and Phytogeography Series, 5(1): 28-37.]

LIU FQ, WANG JS, 2001. Influence of salicylic acid on antioxidant enzymes in rice leaves [J]. Journal of Agricultural Biotechnology, 9(4): 396-399. [LIU Fengquan, WANG Jinsheng, 2001. Effects of salicylic acid on antioxidant enzyme systems in rice leaves [J]. Journal of Agricultural Biotechnology, 9(4): 396-399.]

LIU YX, WU JW, WANG LN, et al., 2023. Physiological and ecological response characteristics of *Pinus yunnanensis* seedlings under drought stress [J]. Molecular Plant Breeding: 1-16[2025-08-08]. https://link.cnki.net/urlid/46.1068.S.20230518.1319.004. [LIU Yunjie, WU Junwen, WANG Lina, et al., 2023. Responses of growth and physiological-biochemical characteristics of *Pinus yunnanensis* seedlings to continuous drought stress [J]. Molecular Plant Breeding: 1-16[2025-08-08]. https://link.cnki.net/urlid/46.1068.S.20230518.1319.004.]

LI XQ, WEN YZ, HUANG CH, et al., 2024. Genetic diversity, mating system, and seed viability reveal a trade-off between outcrossing and inbreeding in *Pinus yunnanensis* var. *tenuifolia*, an ecologically important conifer species growing in a hot-dry river basin habitat in southwest China [J]. Forests, 15(6): 982.

LIAO LL, WEI W, WEN YZ, et al., 2024. Unique geoclimatic factors and topography-shaped pollen flow of *Pinus yunnanensis* var. *tenuifolia* wild populations in the dry-hot river basin in China [J]. Forests, 15(12): 2215.

LUO H, XU H, CHU C, et al., 2020. High temperature can change root system architecture and intensify root interactions of plant seedlings [J]. Frontiers in Plant Science, 11: 160.

PAN YF, YANG MH, LIU WD, et al., 2024. Effects of different formula fertilization on the growth and physiological characteristics of *Quercus chungii* seedlings [J]. Journal of Central South University of Forestry & Technology, 44(6): 69-80. [Pan Yanfei, Yang Mohua, Liu Weidong, et al., 2024. Effects of different formula fertilization on the growth and physiological characteristics of *Quercus chungii* seedlings [J]. Journal of Central South University of Forestry & Technology, 44(6): 69-80.]

POORTER H, NIKLAS KJ, REICH PB, et al., 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control [J]. New Phytologist, 193(1): 30-50.

R CORE TEAM, 2024. R: A Language and environment for statistical computing [M]. Vienna, Austria: R Foundation for Statistical Computing.

SHANG FQ, GAO Y, MA XY, et al., 2024. Variation analysis and evaluation selection of growth and seed traits of *Pinus koraiensis* from different provenances [J]. Seed, 43(10): 74-84. [Shang Fuqiang, Gao Yuan, Ma Xiaoyu, et al., 2024. Variation analysis and evaluation selection of growth traits and seed traits of *Pinus koraiensis* from different provenances [J]. Seed, 43(10): 74-84.]

SANTIAGO LS, WRIGHT SJ, 2007. Leaf functional traits of tropical forest plants in relation to growth form [J]. Functional Ecology, 21(1): 19-27.

SCHNEIDER CA, RASBAND WS, ELICEIRI KW, 2012. NIH Image to ImageJ: 25 years of image analysis [J]. Nature Methods, 9(7): 671-675.

TIAN KX, XU JY, DAI L, et al., 2024. Physiological response of *Idesia polycarpa* seedlings to extreme high temperature and high temperature plus drought stress [J]. Scientia Silvae Sinicae, 60(11): 84-92. [Tian Kaixin, Xu Junyuan, Dai Li, et al., 2024. Physiological responses of *Idesia polycarpa* seedlings to extreme high temperature and combined high-temperature-drought stress [J]. Scientia Silvae Sinicae, 60(11): 84-92.]

TESKEY R, WERTIN T, BAUWERAERTS I, et al., 2015. Responses of tree species to heat waves and extreme heat events [J]. Plant, Cell & Environment, 38(9): 1699-1712.

VARSAMIS G, PAPAGEORGIOU AC, MEROU T, et al., 2019. Adaptive diversity of beech seedlings under climate change scenarios [J]. Frontiers in Plant Science, 9: 1918.

WANG XB, 1991. The phytocoenological features of *pinus yunnanensis* var. *tenuifolia* forest in Guangxi [J]. Bulletin of Botanical Research, 11(3): 91-103. [Wang Xianpu, 1991. Phytocoenological characteristics of *Pinus yunnanensis* var. *tenuifolia* forests in Guangxi [J]. Bulletin of Botanical Research, 11(3): 91-103.]

WEI QM, HUANG YC, ZHAO YH, et al., 2017. Physiological responses of seedlings of *Pinus yunnanensis* var. *tenuifolia* to PEG-6000 simulated drought stress [J]. Journal of Southwest Forestry University (Natural Sciences), 37(3): 7-13. [Wei Qiumei, Huang Yicui, Zhao Yihui, et al., 2017. Physiological responses of *Pinus yunnanensis* var. *tenuifolia* seedlings to PEG-6000 simulated drought stress [J]. Journal of Southwest Forestry University (Natural Sciences), 37(3): 7-13.]

WU DS, TANG X, CEN ZM, et al., 2016. Dynamic analysis of *Pinus yunnanensis* var. *tenuifolia*

forest resources in Guangxi [J]. Guangxi Forestry Science, 45(3): 316–321. [WU Dongshan, TANG Xin, CEN Zuming, et al., 2016. Dynamic analysis of *Pinus yunnanensis* var. *tenuifolia* forest resources in Guangxi [J]. Guangxi Forestry Science, 45(3): 316–321.]

WRIGHT IJ, WESTOBY M, 1999. Differences in seedling growth behaviour among species: trait correlations across species, and trait shifts along nutrient compared to rainfall gradients [J]. Journal of Ecology, 87(1): 85–97.

XU XL, 1983. The geographical distribution and growth characteristics of *Pinus yunnanensis* var. *tenuifolia* forest in Guizhou province [J]. Guizhou Science(1): 91–95. [XU Xueliang, 1983. Geographical distribution and growth characteristics of *Pinus yunnanensis* var. *tenuifolia* forest in Guizhou [J]. Guizhou Science(1): 91–95.]

YANG XJ, LIANG YY, WANG XL, et al., 2024. Phenotypic diversity of wild *Glyptostrobus pensilis* in Guangxi and its relationship with geographical-climatic factors [J]. Journal of Plant Resources and Environment, 33(4): 61–70. [YANG Xiaojing, LIANG Yongyan, WANG Xilong, et al., 2024. Phenotypic diversity of wild *Glyptostrobus pensilis* in Guangxi and its relationship with geographical-climatic factors [J]. Journal of Plant Resources and Environment, 33(4): 61-70.]

YANG ZQ, FENG YH, WU DS, 2014. Analysis of genetic diversity of *Pinus yunnanensis* var. *tenuifolia* nature populations by SSR marker [J]. Guihaia, 34(1): 10-14. [YANG Zhangqi, FENG Yuanheng, WU Dongshan, 2014. SSR analysis of genetic diversity in natural populations of *Pinus yunnanensis* var. *tenuifolia* [J]. Guihaia, 34(1): 10–14.]

YI HT, FANG HX, HUANG ZY, 2017. Effects of three plant growth regulators on seedling physiological indexes of *Pinus yunnanensis* var. seed germination [J]. Modern Agricultural Science and Technology(15): 132–134. [YI Hongtao, FANG Huixin, HUANG Zeyue, 2017. Effects of three plant growth regulators on physiological indexes of seedlings after seed germination of *Pinus yunnanensis* var. *tenuifolia* [J]. Modern Agricultural Science and Technology(15): 132–134.]

ZHAO LJ, QUAN JH, ZHU LQ, et al., 2022. Ecological adaptability of endangered plant *Bhesa robusta* sapling in different habitats [J]. Guihaia, 42(3): 501–509. [ZHAO Lijun, QUAN Jiahui, ZHU Liqiong, et al., 2022. Ecological adaptability of endangered *Bhesa robusta* saplings in different habitats [J]. Guihaia, 42(3): 501–509.]

ZHAO SG, JING Y, YANG JX, 1993. Relation between peroxidase and polyphenol oxidase activities in poplar bark and canker-resistance [J]. Journal of Northwest Forestry College, 8(3): 13–17. [ZHAO Shiguang, JING Yao, YANG Junxiu, 1993. Relationship between peroxidase and polyphenol oxidase activities in poplar bark and resistance to canker disease [J]. Journal of Northwest Forestry College, 8(3): 13–17.]

ZHENG DB, LIU XL, HAN JX, et al., 2022. Research of Natural Regeneration of *Pinus yunnanensis* var. *tenuifolia* of Yachang Forest Farm [J]. Journal of Green Science and Technology, 24(13): 79–81, 84. [ZHENG Dangbin, LIU Xiaolu, HAN Junxue, et al., 2022. Survey and study on natural regeneration of *Pinus yunnanensis* var. *tenuifolia* in Yachang Forest District [J]. Journal of Green Science and Technology, 24(13): 79–81, 84.]

ZHOU RL, PANG JQ, SONG Y, 2021. Physiological response of *Pinus thunbergii* Parl. in wind resistant to coastal wind blowing and win-drift blowing [J]. Acta Ecologica Sinica, 41(5): 2033-2044. [ZHOU Ruilian, PANG Jinqiang, SONG Yu, 2021. Physiological responses of the coastal wind-resistant plant *Pinus thunbergii* to clean wind and wind-sand flow [J]. Acta Ecologica Sinica, 41(5): 2033–2044.]

ZHOU YF, LUO C, LI S, et al., 2025. Effects of broadleaved transformation on stand structure of *Pinus massoniana* forest in subtropical area [J]. Journal of Beijing Forestry University, 47(1): 11–21. [ZHOU Yufei, LUO Chao, LI Sheng, et al., 2025. Effects of broad-leaved transformation of subtropical *Pinus massoniana* forests on stand structure [J]. Journal of Beijing Forestry University, 47(1): 11–21.]

ZHANG YN, ZHUANG Y, WANG XG, et al., 2024. Evaluation of growth, physiological response, and drought resistance of different flue-cured tobacco varieties under drought stress [J]. Frontiers in Plant Science, 15: 1442618.

Note: Figure translations are in progress. See original paper for figures.