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Drought aggravates the negative effects of warming on the growth of drought-intolerant tree seedlings in temperate forests

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Abstract

Background How tree seedlings with contrasting drought tolerance respond to climate change remains largely unexplored, which will limit our ability to predict future forest composition and resilience under shifting climatic conditions. Here, we investigated the effects of warming and interannual precipitation variability on the photosynthetic properties, antioxidant enzyme activities, and growth of two dominant tree species (*Fraxinus mandshurica*, a drought-intolerant species; *Quercus mongolica*, a drought-tolerant species) in a temperate forest through a two-year field warming experiment using an infrared heating system.

Results The infrared treatment increased temperatures by 2 °C in the 0–10 cm soil layer and by 1.49 °C at 0.2 m above the surface (seedling height), accompanied by a 4.45% increase in vapor pressure deficit (VPD) at 0.2 m compared to ambient conditions. In a non-drought year, warming reduced photosystem II performance in both species and significantly increased malondialdehyde content by 67% in *F. mandshurica* seedlings. In a drought year, warming reduced the net photosynthetic rate by 12% in *Q. mongolica* and by 28% in *F. mandshurica*, and also decreased antioxidant enzyme activity in both species. Notably, the growth of *Q. mongolica* was not affected by warming in the non-drought year, whereas warming significantly suppressed the total biomass, root collar diameter increment, and height growth of *F. mandshurica* over two years, with reductions of 30%, 48% and 67% in the drought year, and 33%, 18% and 11% in the non-drought year, respectively. Increased VPD may be a key factor limiting the growth and physiological responses of *F. mandshurica* seedlings under warming conditions.

Conclusions These findings indicate that the effects of warming are species-specific, with drought-intolerant species showing greater sensitivity to projected climate change. Their responses are further intensified under drought conditions, underscoring their heightened vulnerability in a warming climate.

Keywords Warming, Drought-intolerant species, Precipitation, Growth, Photosynthesis, Antioxidant enzyme

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Introduction

Anthropogenic greenhouse gas emissions, such as carbon dioxide (CO_2), have driven an increase in global mean surface air temperatures, which are predicted to increase by 4 °C by the year 2100 (IPCC 2021). Climate change not only increases surface temperatures but also alters the timing and spatial distribution of precipitation and evapotranspiration (Su et al. 2022; Wei et al. 2023). Additionally, precipitation intensity is expected to become more variable (Wang et al. 2014). All above-mentioned alterations significantly affect soil water availability for plants (Dai et al. 2021). Under the background of warming, increasingly severe and frequent drought events are expected to pose a major risk to forest ecosystems (Clark et al. 2016; Vicente-Serrano et al. 2020). Therefore, taking into account the inter-annual fluctuations in precipitation is crucial for accurately forecasting forest dynamics and modeling carbon and water cycles amid the ongoing warming trend. Temperate forests, located in regions experiencing sensitive and rapid climate warming, are typically limited by temperature, precipitation, and nutrient availability (Landuyt et al. 2019; Kasel et al. 2022). Consequently, a warmer climate accompanied by abundant precipitation is expected to enhance the productivity of temperate forest ecosystems (Tang et al. 2023).

Rising temperatures are likely to alleviate enzymatic limitations on photosynthetic biochemistry in temperate forests (Zhao et al. 2022; Jiao et al. 2024), potentially enhancing tree growth through increased photosynthetic activity. However, under warming conditions, carbon dioxide assimilation may decline if soil moisture limitations induce stomatal closure, thereby reducing CO_2 availability for photosynthesis (Reich et al. 2018). Climate warming can positively impact tree growth when soil moisture is adequate, but may have adverse effects during periods of soil dryness. Moreover, since temperature and soil moisture effects are interdependent (Hammond et al. 2022; Lu et al. 2022), the overall impact of warming on tree growth and its underlying mechanisms remains unclear.

As global warming accelerates the frequency of drought events, species' varying drought tolerances will play a critical role in shaping forest community responses to climate change. As a byproduct of aerobic metabolism in plants, reactive oxygen species (ROS) maintain a dynamic equilibrium between production and scavenging under normal conditions. However, under severe drought stress, this balance is disrupted, leading to the accumulation of ROS and consequent oxidative damage to plant cells (Noctor et al. 2014; Baladrón et al. 2023). Under drought stress, plants can upregulate antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and ascorbate peroxidase (APX), as well as increase osmolytes like proline to mitigate ROS damage (Zhang et al. 2018; Wang et al. 2021). The upregulation of antioxidant enzyme activities has been linked to enhanced drought tolerance in plants (Islam et al. 2021). Although antioxidant systems play a crucial role in mitigating drought stress, their involvement in regulating tree growth responses to drought under warming conditions remains poorly understood. Furthermore, the accumulation of ROS also results in lipid peroxidation and thus exerts negative impacts on the photosystem II reaction center (triggering photoinhibition), and key photosynthetic components such as Rubisco enzyme, thereby further reducing photosynthetic rates (Foyer 2018). Drought-intolerant species tend to close their stomata at relatively high water potentials (Tardieu and Simonneau 1998), resulting in decreased photosynthesis, reduced photochemical quantum yield of PSII (Y(II)), impaired growth, and diminished non-structural carbohydrate (NSC) storage during drought (Dickman et al. 2014; Manrique-Alba et al. 2018; Song et al. 2025). Drought-tolerant species can acclimate to low soil moisture by optimizing carbon uptake efficiency under restrictive conditions, involving cellular adjustments that reduce transpiration rates and enhance water use efficiency to minimize water loss (reviewed in Bréda et al. 2006; Niinemets 2010; Jiang et al. 2024). A temperature increase of + 5.0 °C enhanced photosynthetic efficiency and carbon uptake in oak trees (a drought-tolerant species) (Grossiord et al. 2022). In contrast, carbon uptake in beech (a drought-intolerant species) declined under warming conditions, primarily due to a substantial reduction in stomatal conductance during periods of limited soil moisture (Grossiord et al. 2022). Consequently, warming can exert varying effects on photosynthetic traits and tree growth depending on a species' drought tolerance.

Compared to adult trees, woody plant seedlings represent the most vulnerable developmental stage in their life cycle and are more sensitive to environmental changes (Lloret et al. 2009). Seedling early growth responses to environmental factors can partially determine vegetation abundance, distribution patterns, and population regeneration success (Tripathi et al. 2020; Yuan et al. 2022; McNichol and Russo 2023; Du et al. 2024). Therefore, investigating the effects of warming on the early growth and physiology of seedlings of major tree species in temperate secondary forests is crucial for predicting their future developmental trajectories under climate change.

This study was carried out over two consecutive years on a field platform with *in-situ* infrared heating, encompassing both drought and non-drought conditions. It aimed to explore the effects of warming on the growth

and physiological characteristics of *Fraxinus mandshurica* Rupr. and *Quercus mongolica* Fisch. ex Ledeb., which are commercial timber species in the temperate forests of Northeast China. *Q. mongolica* mainly distributes in the xeric environment with sunny slopes and at high elevations, and is a drought-tolerant species (Dai et al. 2020). In contrast, *F. mandshurica* is a drought-intolerant species and tends to grow in comparatively humid sites such as river banks and shady slopes (Liu et al. 2015; Yuan et al. 2023). Our objectives were to determine how interannual changes in precipitation, coupled with warming, affected the response of photosynthesis, enzyme activity, and growth of two species with different drought tolerances. We suppose that (1) in normal precipitation year, *F. mandshurica* and *Q. mongolica* will have higher leaf-level photosynthesis, growth, and lower antioxidant enzyme activity with warming; (2) in drought year, warming will decrease the photosynthesis and growth of both species, but larger reductions are expected in *F. mandshurica*. Species with high drought tolerance are likely to better withstand future climate conditions, while those with low drought tolerance may face a higher risk of extinction, thereby impacting the diversity and stability of ecosystems. By fully considering the drought tolerance of tree species, this paper will reveal the underlying mechanisms behind the growth changes of seedlings under warming conditions.

Materials and methods

Study site

The experiment was conducted at the Qingyuan Forest CERN (Chinese Ecosystem Research Network), National Observation and Research Station (N41°51′9.94″, E124°56′11.22″), using an in situ infrared heating (IR) system for field warming. The station is situated in the montane region of eastern Liaoning Province, Northeast China. The area experiences a continental monsoon climate characterized by humid, rainy summers and cold, snowy winters, with a mean monthly temperature of 21 °C in July and − 12.1 °C in January. The mean annual air temperature is approximately between 3.9 and 5.4 °C. The mean annual precipitation is 811 mm, with approximately 80% occurring between June and August (Yuan et al. 2023).

In 2019, precipitation was evenly distributed throughout the growing season from May to August, whereas in 2020, a prolonged drought occurred during the growing season, with consecutive rainless periods lasting up to 23 days in June and 18 days in July (Fig. S1). Soil relative humidity was used as an indicator of drought assessment (Wei et al. 2022). Monitoring and calculations showed that soil relative humidity from June to August was consistently above 60% in 2019 (non-drought year), whereas it ranged between 40 and 60% in 2020 (drought year).

Experiment design

The warming platform consisted of six rectangular plots (18 m × 6 m) on a northwest-facing slope, separated by 5–15 m buffer zones, with three plots subjected to a + 2 °C warming treatment and three serving as controls (Duan et al. 2022). In each warming plot, rod-shaped infrared heaters, Model HS-2420 (Kalglo Electronics Co. Inc., Bethlehem, PA, USA), 8 mm in diameter and 151 cm in length, 2,000 W, 240 V, were mounted in an equilateral triangular frame and operated continuously to warm vegetation and soil surfaces, simulating natural climate warming. To monitor subsoil temperature and moisture, a set of probes, Campbell CS655, with data logger CR1000 (Campbell Scientific, Logan, UT, USA) was installed at depths of 5, 10, 20, 30, and 40 cm at the center of each plot, with one probe for each soil layer of the plot. Additionally, an air temperature (T_{air}) and air relative humidity (RH) meteorological station (Onset Computer Corporation, Bourne, MA, USA) was installed in a warmed plot and in a control plot to record air temperature and humidity at heights of 0.2, 0.5, and 1.0 m. The calculation of vapor pressure deficit (VPD) followed the method described by Arain et al. (2022).

In each large experimental plot (6 m × 18 m), a 2 m × 2 m square was established for seedling transplantation. In late August 2018, uniform one-year-old seedlings of *Q. mongolica* and *F. mandshurica*, matched in size and height, were collected from areas adjacent to the Qingyuan Forest CERN (Fig. S2) and transplanted into the squares. A total of 80 seedlings per species were planted in each square, with a fixed spacing of 15 cm between individuals to ensure consistent growing conditions. The *Q. mongolica* seedlings had an average root collar diameter of 1.27 ± 0.07 mm and height of 12.41 ± 0.46 cm, while *F. mandshurica* seedlings measured 1.14 ± 0.06 mm in diameter and 10.13 ± 0.23 cm in height.

From each square, four representative seedlings of *Q. mongolica* and *F. mandshurica* were selected and permanently marked for subsequent measurements. Gas exchange measurements were conducted on fully expanded leaves of seedlings (four seedlings per species per plot) using a portable open-path gas exchange system, LI-6400 (LI-COR Inc., Lincoln, NE, USA) between 09:00 and 11:30 a.m. on clear days in early August of 2019 and 2020. The LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE, USA) was equipped with a standard 2 cm × 3 cm leaf chamber and an integrated LED light source. During measurements, leaves were

exposed to a constant photosynthetic photon flux density (PPFD) of 1200 μmol m^{-2} s^{-1}, an ambient CO_2 concentration of 400 ppm, and relative humidity maintained between 50 and 70% within the chamber. Net photosynthetic rate (P_n), stomatal conductance (Cond), and transpiration rate (T_r) were measured over three consecutive days. Subsequently, instantaneous leaf water use efficiency (WUE) and stomatal limitation (Ls) were calculated from the measured gas exchange parameters using the following formulas (Fang et al. 2023).

On clear days in early August of 2019 and 2020, the maximum photochemical efficiency of PSII (F_v/F_m), relative electron transport rate (ETR), actual photochemical efficiency of PSII (Y(II)), and photochemical quenching coefficient (qP) were measured using an FMS-2 pulse-modulated fluorometer (Hansatech Instruments Ltd., Norfolk, UK). Gas exchange and chlorophyll fluorescence parameters were determined on the same leaves. Before measurement, leaves were dark-adapted for 30 min using a clip. The minimal fluorescence (F_o) was determined under a weak modulated light (0.03 μmol m^{-2} s^{-1}), and the maximal fluorescence (F_m) was obtained by applying a saturating pulse of light (6000 μmol m^{-2} s^{-1}, over 0.8 s). Subsequently, leaves were light-adapted for five minutes under continuous actinic light (200 μmol m^{-2} s^{-1}), the corresponding fluorescence (F) was monitored, and maximal fluorescence of the light-adapted state (F_m') was recorded using a saturating pulse. F_v/F_m, Y(II), ETR, and qP were calculated following the methods described by Maxwell and Johnson (2000).

In early August 2019 and 2020, during the peak growing season, middle and upper canopy leaves were randomly sampled from four seedlings per species within each square. The collected leaves were immediately placed in gauze bags and flash-frozen in liquid nitrogen. The frozen leaves were ground into fine powder under liquid nitrogen and stored at − 80 °C for analysis. Malondialdehyde (MDA) content was determined using the TBA assay following Dhindsa et al. (1981). Proline content was determined following Bates et al. (1973). Superoxide dismutase (SOD) activity was determined using the xanthine oxidase method (Giannopolitis and Ries 1977). Peroxidase (POD) activity was measured using the guaiacol method (Kochhar et al. 1979). Catalase (CAT) activity was assessed using a modified ultraviolet absorption method based on Kraus and Fletcher (1994). The modifications to Kraus and Fletcher (1994) include using a lower centrifugation speed (3000 rpm for 15 min) and a smaller sample volume (0.5 μL). Ascorbate oxidase (AAO) activity was determined following Esaka et al. (1990).

In early September of 2018, 2019, and 2020, growth parameters, including root collar diameter and seedling height, were measured for 50 seedlings per species using a caliper and a ruler, respectively. The growth increments for root collar diameter (RCD_{inc}) and height (H_{inc}) in 2019 and 2020 were calculated as the difference between the measured values of the current year and the previous year. Furthermore, eight seedlings of *Q. mongolica* and *F. mandshurica* were harvested for each square. The entire seedlings were carefully excavated with a small shovel, and their roots were gently cleaned with distilled water to minimize damage. Based on the maximum root length (*Q. mongolica*: 11.84 ± 0.39 cm and *F. mandshurica*: 6.25 ± 0.39 cm) and the average increment in root growth under optimal conditions (approximately 7 cm) over a complete growing season (Yuan et al. 2022), the maximum excavation depths in 2019 and 2020 were 25 cm and 35 cm, respectively, to ensure that the entire root system was collected. Subsequently, the seedlings were separated into roots, stems, and leaves. Leaves from both species were harvested. The leaves were scanned using a high-resolution scanner (Founder Z1600, China), and the leaf area was quantified with image processing software (Adobe Photoshop CS4). Following scanning, the leaves, stems and roots were initially heated at 105 °C for 30 min, then oven-dried at 65 °C until a constant weight was attained. The root-to-shoot ratio was determined as the ratio of root mass to shoot mass (Yuan et al. 2022). Specific leaf area (SLA) was calculated based on the dry weight of the leaves (Shah et al. 2024; Tian et al. 2024). The dried leaves were ground using a ball mill, and coarse particles were removed by passing the powder through a 60 μm sieve. Leaf carbon and nitrogen contents were quantified using an elemental analyzer (Vario EL III, Elemental Analysis System GmbH, Germany).

A total of 50 seedlings were used to measure root collar diameter and height, after which they were divided into five replicates. From each square, four seedlings of each species were selected and marked for gas exchange and chlorophyll fluorescence measurements. Additionally, eight seedlings from each square were harvested and divided into four replicates. These seedlings were first used to measure leaf area and SLA, and then dried to measure total biomass, leaf carbon, and nitrogen content. Fresh leaves were randomly sampled from four seedlings per species within each square to determine MDA and proline contents, as well as the activities of SOD, POD, CAT, and AAO.

Data analysis

Duan et al. (2022) investigated the effects of warming on soil temperature and soil moisture in the study area. Compared to the control, the infrared radiation heating system elevated surface soil temperature (0–10 cm) by approximately 2 °C, aligning with our experimental

target, except during periods of heavy rainfall and power outages. However, soil moisture at the forest site showed no significant response to warming; therefore, its impact on seedling growth and physiology was not further examined (Fig. S3) (Duan et al. 2022). With T_{air} and RH monitored in just one warming and one control plot, only the observed changes in these variables and VPD are reported.

Data were assessed using the Kolmogorov–Smirnov test for normality and Levene's test for homogeneity of variance before statistical analysis. When the data did not conform to the assumption of normality and homogeneity of variances, they were logarithmically transformed. A two-way analysis of variance (ANOVA) was used to examine the effects of warming and tree species on seedling growth characteristics (Biomass, RCD_{inc}, and H_{inc}), morphological traits (total leaf area and SLA), and physiological indicators (gas exchange parameters: P_n, T_r, Cond, WUE, Ls; chlorophyll fluorescence: F_v/F_m, ETR, Y(II), qP; leaf nutrients: leaf nitrogen, leaf carbon-to-nitrogen ratio; malondialdehyde and proline; antioxidant enzymes: SOD, CAT, POD, AAO). The two-way ANOVA was performed using the nlme package in R version 4.3.1 (R Core Team 2021).

Principal component analysis (PCA) was used to analyze interrelations of variables for *Q. mongolica* and *F. mandshurica*, respectively, using the "Stats" package in R (version 4.3.1; R Foundation for Statistical Computing). The statistical results were considered significant at $P < 0.05$.

A partial least squares path modeling (PLS-PM) was constructed to further explore the causal relationships among warming, photosynthesis, chlorophyll fluorescence, foliar morphology, antioxidant enzymes, and growth for *Q. mongolica* and *F. mandshurica.* The models were constructed using the "innerplot" function in the "plspm" package in R.

Results

Environmental variables after warming

The effects of warming on soil temperature and soil moisture have been previously reported (Fig. S3; Duan et al. 2022). In 2019 and 2020, air temperature (T_{air}) at 0.2 m under the warming treatment increased by 1.44 ± 0.05 °C and 1.53 ± 0.05 °C, respectively, compared to the control (Fig. S4). RH at 0.2 m decreased by 6.85 ± 0.26% in 2019 and 6.44 ± 0.33% in 2020 under warming relative to the control (Fig. S4). Additionally, the average monthly VPD at 0.2 m increased by 3.5% and 5.4% in 2019 and 2020, respectively, under warming compared to the control treatment (Fig. S4).

Effects of warming on growth, morphological and physiological characteristics of seedlings

The increments of root collar diameter of *F. mandshurica* seedlings under control were higher than those of

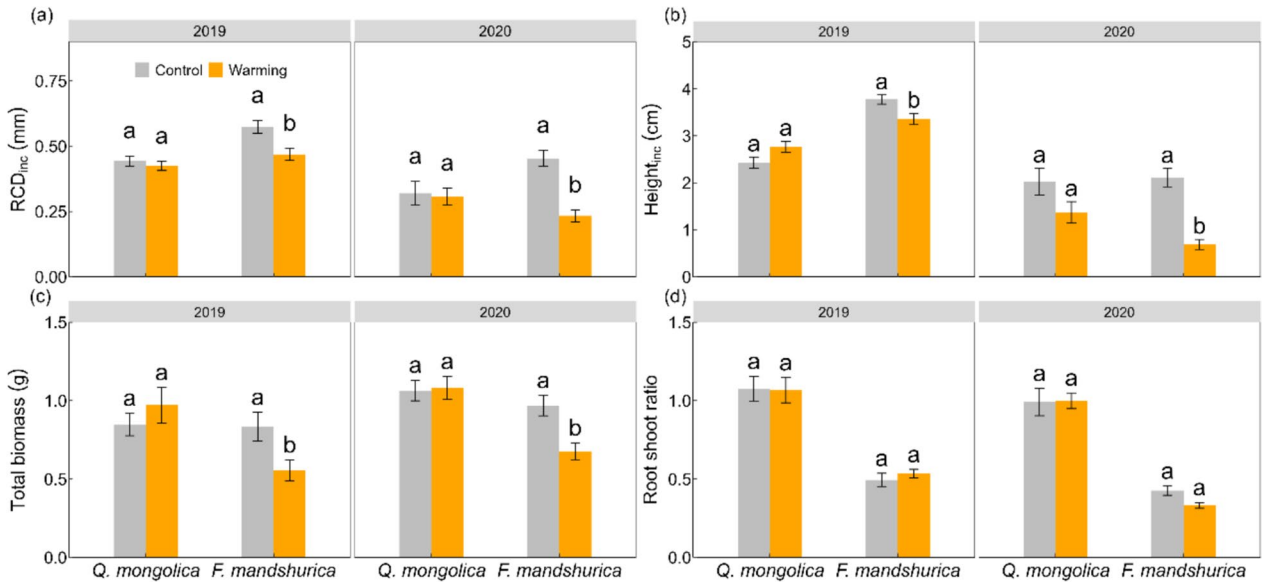


Fig. 1 The mean periodic increment in root collar diameter (RCD_{inc}, mm, $n = 5$) (**a**), mean periodic increment in height ($Height_{inc}$, cm, $n = 5$) (**b**), total biomass (g, $n = 5$) (**c**), and root shoot ratio ($n = 5$) (**d**) for different species growing under the two temperatures (control; + 2 ℃). 2019 was a normal precipitation year, and 2020 was a drought year. The data were presented as the mean ± S.E. Different lowercase letters indicated significant differences ($P < 0.05$) between temperature treatments for the same species

the warming in 2019 and 2020 (Fig. 1a). The increments of height of *F. mandshurica* under warming were both significantly lower than those of the control in 2019 and 2020 (Fig. 1b).S

In 2019, temperature, tree species, and their interactions had significant effects on seedling biomass ($F=4.037$, $P<0.05$; $F=13.262$, $P<0.001$; $F=5.489$, $P<0.05$) (Table S1). In 2020, tree species, the interaction of temperature and tree species had significant effects on seedling biomass ($F=6.361$, $P<0.05$; $F=5.300$, $P<0.05$) (Table S1). In 2019 and 2020, warming significantly decreased the biomass of *F. mandshurica* by 30.1% and 33.5% compared with the control, respectively (Fig. 1c).

Only tree species affected root/shoot ratio in 2019 and 2020 ($F=122.813$, $P<0.001$; $F=91.394$, $P<0.001$) (Table S1; Fig. 1d). Relative to control, warming decreased total leaf area of *F. mandshurica* by 36.6% and 39.9% in 2019 and 2020, respectively (Fig. 2a). Similarly, compared with the control, warming decreased the specific leaf area of *F. mandshurica* by 31.3% and 34.9% in 2019 and 2020, respectively (Fig. 2b).

In 2019, temperature, tree species, and their interactions significantly influenced the net photosynthetic rate in 2020 (Table S2; Fig. 3a). Warming of 2020 reduced the net photosynthetic rate of *Q. mongolica* and *F. mandshurica* by 11.97% and 28.11% relative to control, respectively (Fig. 3a). Compared with the control, transpiration rate of *Q. mongolica* seedlings significantly decreased by 27.5% and 22.97% after warming in 2019 and 2020, respectively (Fig. 3b). Temperature, tree species, and their interaction had significant effects on stomatal conductance of seedlings in 2020 ($P<0.001$) (Table S2). Warming decreased the stomatal conductance of *Quercus mongolica* and *F. mandshurica* seedlings by 30.88% and 35.17% in 2020, respectively (Fig. 3c).

Relative to the control, warming in 2019 only significantly increased the leaf instantaneous water use efficiency by 19.04% for *Q. mongolica*, while warming in 2020 greatly reduced it by 32.26% for *F. mandshurica* (Fig. 3d). However, stomatal limitation of *Q. mongolica* and *F. mandshurica* seedlings was significantly increased by 18.72% and 7.25% after warming in 2020, respectively (Fig. 3e).

In 2019, temperature and tree species significantly affected the F_v/F_m ($F=4.737$, $P<0.05$) and PSII ($F=11.344$, $P<0.01$) of the two species (Table S3). In 2020, only temperature significantly affected F_v/F_m ($F=10.562$; $P<0.01$) (Table S3). The maximum

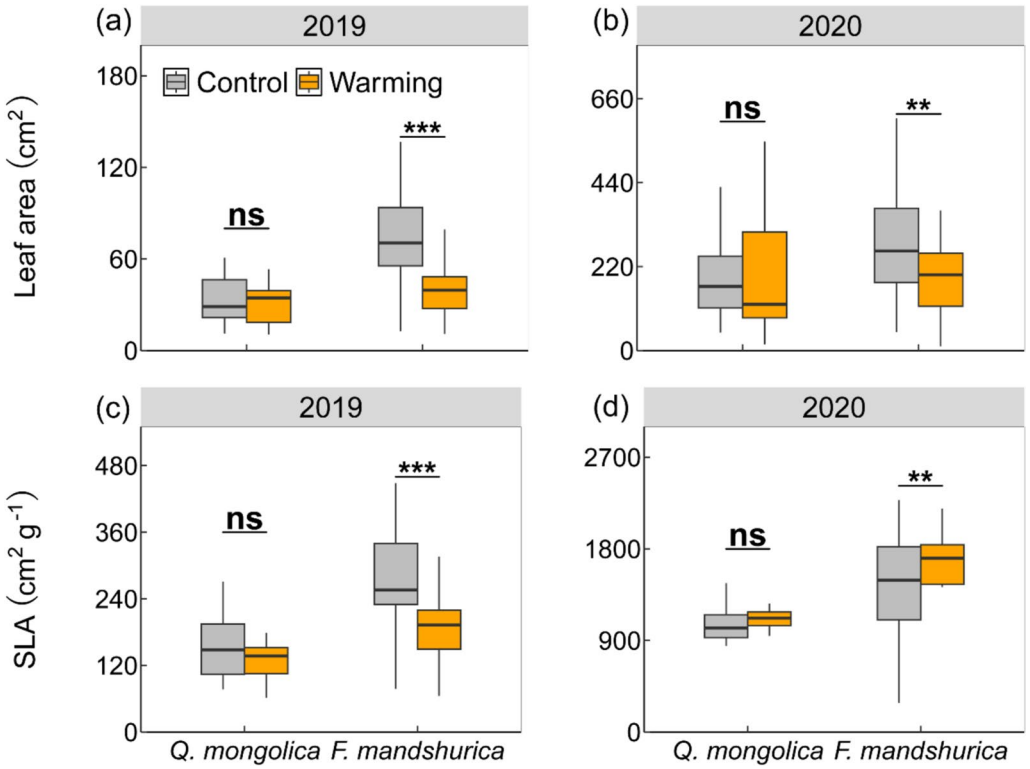


Fig. 2 The leaf area (cm^2, $n=4$) (**a**, **b**) and specific leaf area ($cm^2\ g^{-1}$, $n=4$) (**c**, **d**) for different species growing under the two temperatures (control; + 2 ℃). 2019 was a normal precipitation year, and 2020 was a drought year. The data were presented as the mean ± S.E. ** $P < 0.01$, *** $P < 0.001$, ns not significant

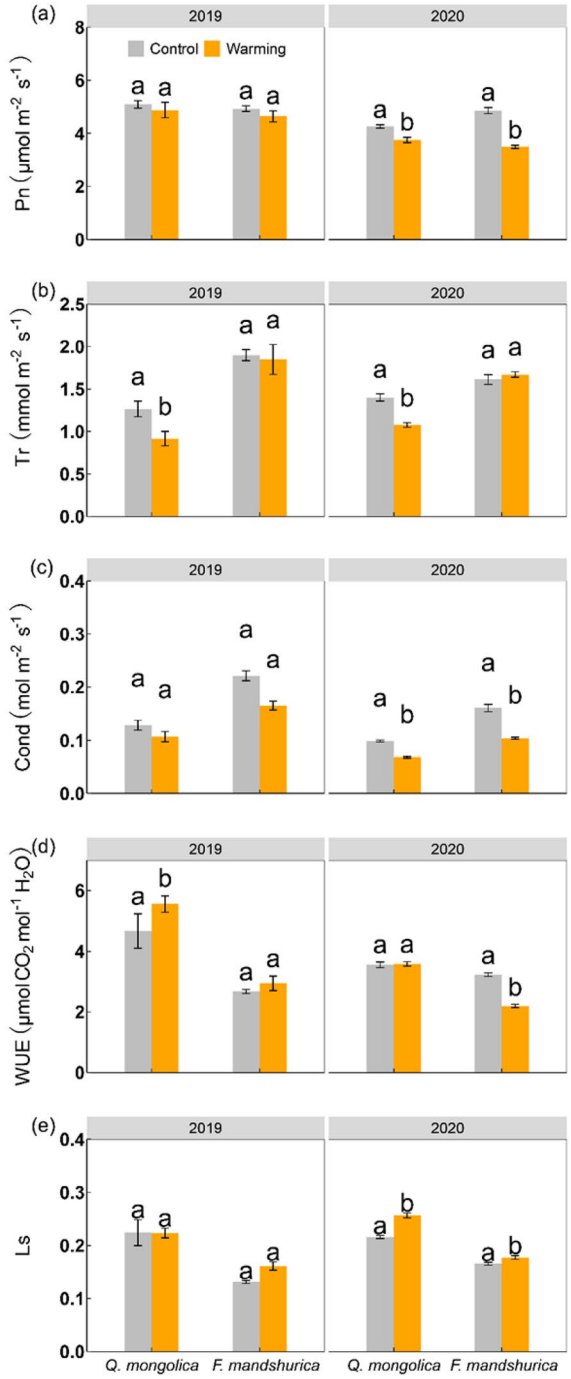


Fig. 3 The net photosynthetic rate (P_n, μmol m^{-2} s^{-1}, $n=4$) (**a**), transpiration rate (T_r, mmol m^{-2} s^{-1}, $n=4$) (**b**), stomatal conductance (Cond, mol m^{-2} s^{-1}, $n=4$) (**c**), water use efficiency (WUE, μmol CO_2 mol^{-1} H_2O, $n=4$) (**d**), and stomatal limit value (Ls, $n=4$) (**e**) for different species growing under the two temperatures (control; + 2 ℃). 2019 was a normal precipitation year, and 2020 was a drought year. The data were presented as the mean ± S.E. Different lowercase letters indicated significant differences ($P<0.05$) between temperature treatments for the same species

photochemical efficiency of PSII in *Q. mongolica* was promoted with increased temperature (Fig. 4a).

In 2019, warming decreased the ETR and Y(II) of *Q. mongolica* by 24.65% and 26.51%, respectively, while decreased by 29.96% and 25.3% for *F. mandshurica,* respectively (Fig. 4b–c). In 2019, photochemical quenching coefficients (qP) of *Q. mongolica* and *F. mandshurica* seedlings were reduced by 24.95% and 25.78% after warming, respectively. In 2020, the qP of two species showed an obvious decreasing trend with increased temperature (Fig. 4d).

In 2019 and 2020, only the tree species had significant effects on leaf N content and leaf C/N ($P<0.05$) (Table S3). Leaf N content (2.63 mg g^{-1}) of *F. mandshurica* seedlings was slightly higher than that of *Q. mongolica* seedlings (2.41 mg g^{-1})(Fig. S5). The leaf C/N (19.62) of *Q. mongolica* was slightly higher than that of *F. mandshurica* (16.48) (Fig. S5).

In 2019 and 2020, temperature significantly influenced the MDA content ($F=8.706$, $P<0.01$; $F=21.945$, $P<0.001$) (Table S4). Warming increased MDA content by 67.21% for *F. mandshurica* in 2019 (Fig. 5a). In 2020, MDA contents of *Q. mongolica* and *F. mandshurica* seedlings increased by 36.59% and 23.71% after warming, respectively (Fig. 5a). The proline content of *F. mandshurica* seedlings showed a decreasing trend after warming in 2020 (Fig. 5f).

Warming decreased SOD activity by 27.03% and 38.57% for *F. mandshurica* in 2019 and 2020, respectively (Fig. 5b). In 2019 and 2020, warming decreased CAT activity by 16.60% and 17.42% for *Q. mongolica* seedlings (Fig. 5c), while decreased by 13.86% and 17.50% for *F. mandshurica* seedlings (Fig. 5c).

The PCA results showed two major dimensions along which traits for *Q. mongolica* and *F. mandshurica* seedlings varied (Fig. 6). For *Q. mongolica* seedlings, PCA1 explained 33.2% of the variation in variables. The positive side of PCA1 loaded variables with higher ETR, Y(II), Biomass, $H_{inc,}$ and SLA (Fig. 6a). Biomass, $RCD_{inc,}$ and H_{inc} were positively influenced by P_n, root shoot ratio, and SLA, whereas these growth parameters were negatively influenced by WUE (Fig. 6a). As for *F. mandshurica* seedlings, the PCA1 explained 28.9% of the variation in variables (Fig. 6b). The positive side of PCA1 loaded variables with higher Photo and SLA. The PCA2 explained 21.7% of the variation. Biomass, RCD_{inc}, H_{inc}, Photo, and WUE were loaded on the positive side, while the negative side of PCA1 loaded variables with higher Ls and SOD (Fig. 6b). Biomass, RCD_{inc}, and H_{inc} were positively correlated with P_n and WUE (Fig. 6b).

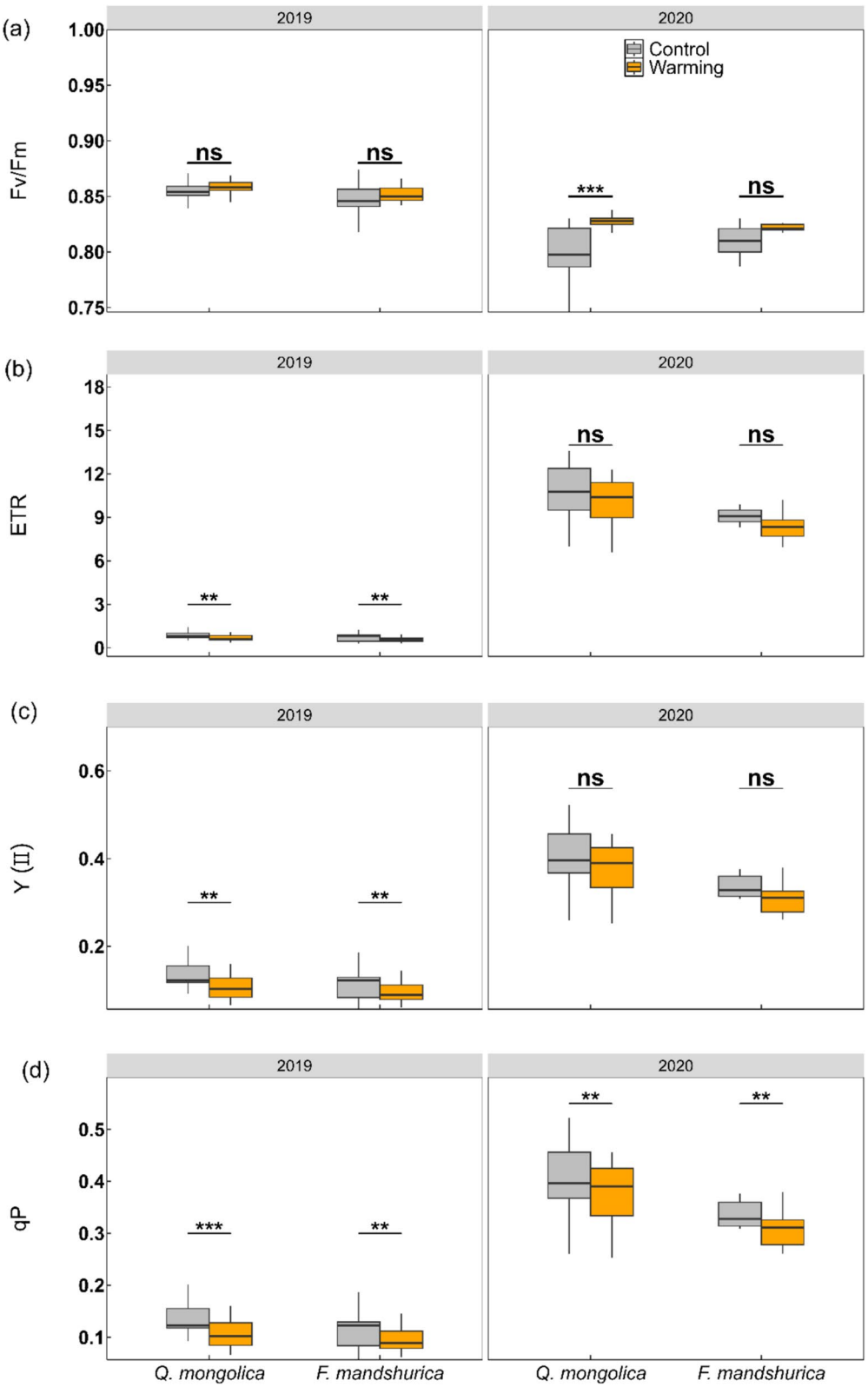


Fig. 4 The F_v/F_m (**a**, $n=4$), ETR (**b**, $n=4$), Y(II) (**c**, $n=4$), and qP (**d**, $n=4$) for different species growing under the two temperatures (control; + 2 ℃). 2019 was a normal precipitation year, and 2020 was a drought year. The data were presented as the mean ± S.E. ** $P < 0.01$, *** $P < 0.001$, ns not significant. F_v/F_m, maximum PSII quantum; ETR, electron transport rate; Y(II), effective PSII quantum Y(II); qP, coefficient of photochemical quenching

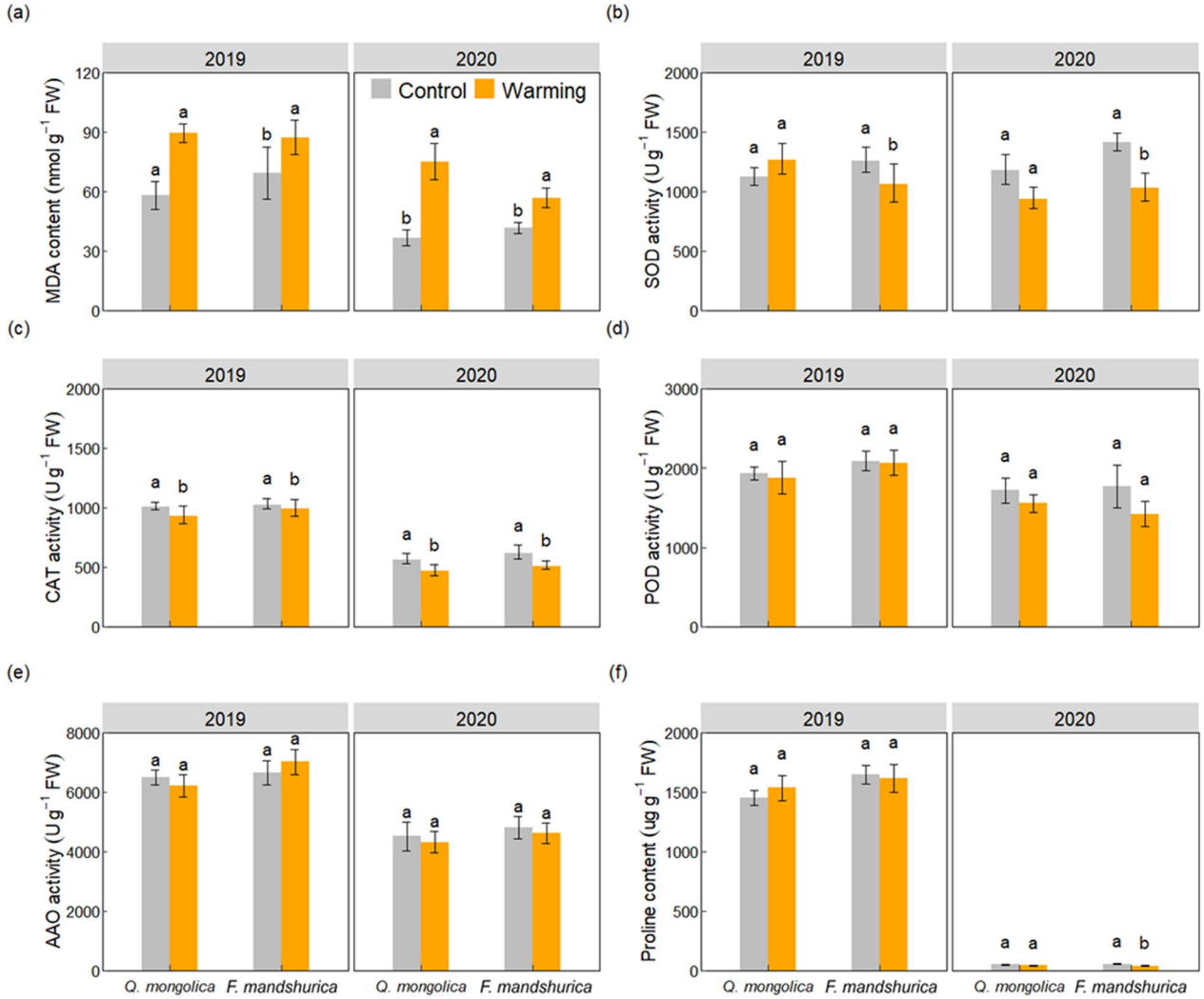


Fig. 5 The MDA content (nmol g^{-1} FW, $n=4$) (**a**), SOD activity (U g^{-1} FW, $n=4$) (**b**), CAT activity (U g^{-1} FW, $n=4$) (**c**), POD activity (U g^{-1} FW, $n=4$) (**d**), AAO activity (U g^{-1} FW, $n=4$) (**e**), and proline content (μg g^{-1} FW, $n=4$) (**f**) for different species growing under the two temperatures (control; + 2 ℃). 2019 was a normal precipitation year, and 2020 was a drought year. The data were presented as the mean ± S.E. Different lowercase letters indicated significant differences ($P<0.05$) between temperature treatments for the same species. MDA, malondialdehyde; SOD, superoxide dismutase; CAT, catalase; POD, peroxidase; AAO, ascorbate oxidase

The direct and indirect effects of warming on seedling growth

A PLS-PM model was conducted to investigate the direct and indirect effects of warming on the growth of two species. In 2019 and 2020, warming treatment significantly affected the chlorophyll fluorescence and photosynthesis of *Q. mongolica* seedlings, respectively ($P<0.001$) (Fig. 7a–b). For *F. mandshurica* seedlings, their growth, chlorophyll fluorescence, and SLA were directly impacted by the warming treatment in 2019 (Fig. 7c). In 2020, the PLS-PM indicated the change in photosynthesis induced by warming, which ultimately affected the growth of *F. mandshurica* seedlings. The total effects of chlorophyll fluorescence (-0.92) and photosynthesis (0.85) were most strongly correlated with the growth of *F. mandshurica* seedlings (Fig. 7d).

Discussion

Effects of warming on seedling growth in a non-drought year

As we initially expected, the effects of warming on seedling growth were species-specific, i.e., warming had no significant impact on the growth of *Q. mongolica*, whereas it reduced the increase in growth of *F.*

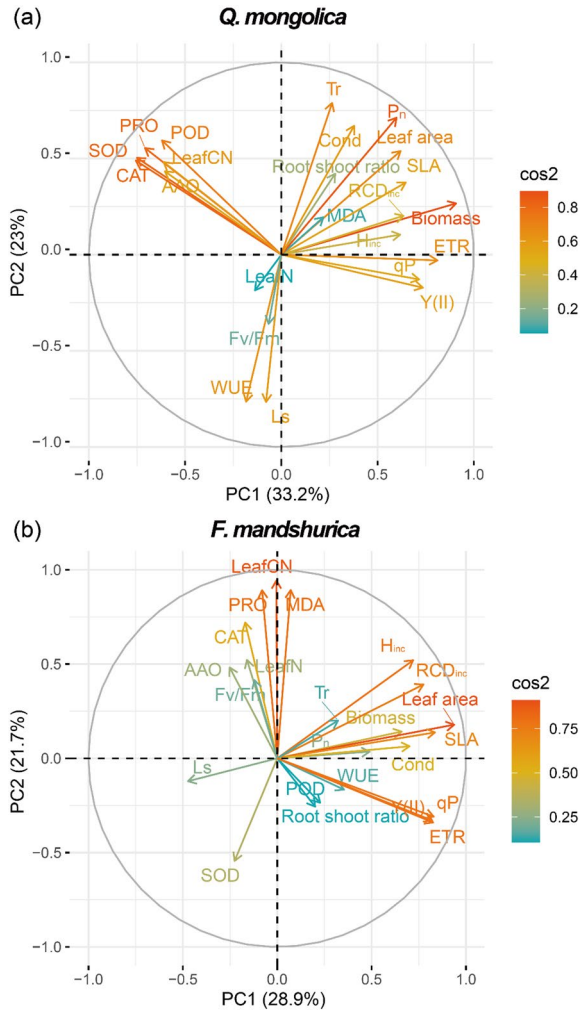


Fig. 6 Principal component analysis (PCA) for growth,morphological and physiological characteristics for *Q. mongolica* (**a**) and *F. mandshurica* (**b**) for the first two axes. Characteristic abbreviations are the same as those in Abbreviations

mandshurica. This finding does not support our initial hypothesis and suggests that *F. mandshurica* is more sensitive to warming than *Q. mongolica*. This is probably due to the broader optimal temperature range and better adaptability to the warming of *Q. mongolica* (Yuan et al. 2022; Liu et al. 2024). Furthermore, warming may increase the dark respiration rate of leaves while decrease the ratio of photosynthetic rate to dark respiration, ultimately leading to reduced biomass accumulation (Fig. 1c) (Liu et al. 2020). Under the warming treatment, the average temperature between 09:00 and 16:00 during the peak growing season (i.e., July and August) was approximately 22–24 °C (Huang et al. 2022). In our previous study conducted in a growth chamber at the same site, we found that warming treatments (+2 °C and +4 °C) increased the total biomass of *F. mandshurica* seedlings compared to the control (Yuan et al. 2022). Therefore, we propose that elevated temperature alone does not constitute a heat stressor that limits the growth of *F. mandshurica*. The contrasting result may be attributed to warming-induced increases in VPD (Grossiord et al. 2020). Furthermore, warming reduced the leaf area and SLA of *F. mandshurica* (Fig. 6a). The warming-induced reduction in SLA of *F. mandshurica* may result from increased leaf thickness (Zhu et al. 2020), which likely facilitates water conservation and improves adaptation to the elevated VPD associated with warming (Michaletz et al. 2015; Wu et al. 2022). In our study, warming reduced RH in 2019 and increased VPD and MDA levels in *F. mandshurica*. These changes suggest that higher VPD under warming may negatively affect *F. mandshurica* by increasing water stress, which could reduce the increase in growth (such as reduced photosynthesis and smaller leaf area), which is consistent with Hsiao et al. (2019). These findings indicate that *F. mandshurica* may be negatively impacted by VPD under warming conditions, potentially leading to diminished growth performance. Moreover, warming reduced the transpiration rate and increased water use efficiency of *Q. mongolica* seedlings, while having no significant effect on these traits of *F. mandshurica* seedlings. This result is partially consistent with our expectation and may be attributed to the greater drought tolerance of *Q. mongolica* seedlings. As a drought-tolerant species, *Q. mongolica* may exhibit a stronger capacity to adjust water use efficiency in response to elevated VPD under warming conditions, compared to the drought-intolerant *F. mandshurica* seedlings. Additionally, we observed reductions in ETR, Y(II), and qP in both species, while F_v/F_m remained unchanged. This indicates that photosystem II (PSII) was not damaged and that the seedlings likely adapted to elevated VPD by modulating light energy utilization and downregulating electron transport through decreased ETR (Martinez et al. 2014; Swoczyna et al. 2022).

The MDA content in the leaves of *F. mandshurica* increased with rising temperature, whereas no such change was observed in *Q. mongolica*, suggesting that *F. mandshurica* experienced oxidative damage induced by elevated temperatures. Elevated MDA levels combined with reduced SOD and CAT activities under warming conditions suggest that *F. mandshurica* seedlings were unable to maintain physiological homeostasis in response to warming-induced stress (Shen et al. 2019; Sun et al. 2020; Guo et al. 2023). We found that the MDA content was positively related to proline content and the C/N of the leaves (Fig. 6b). The results suggest that proline

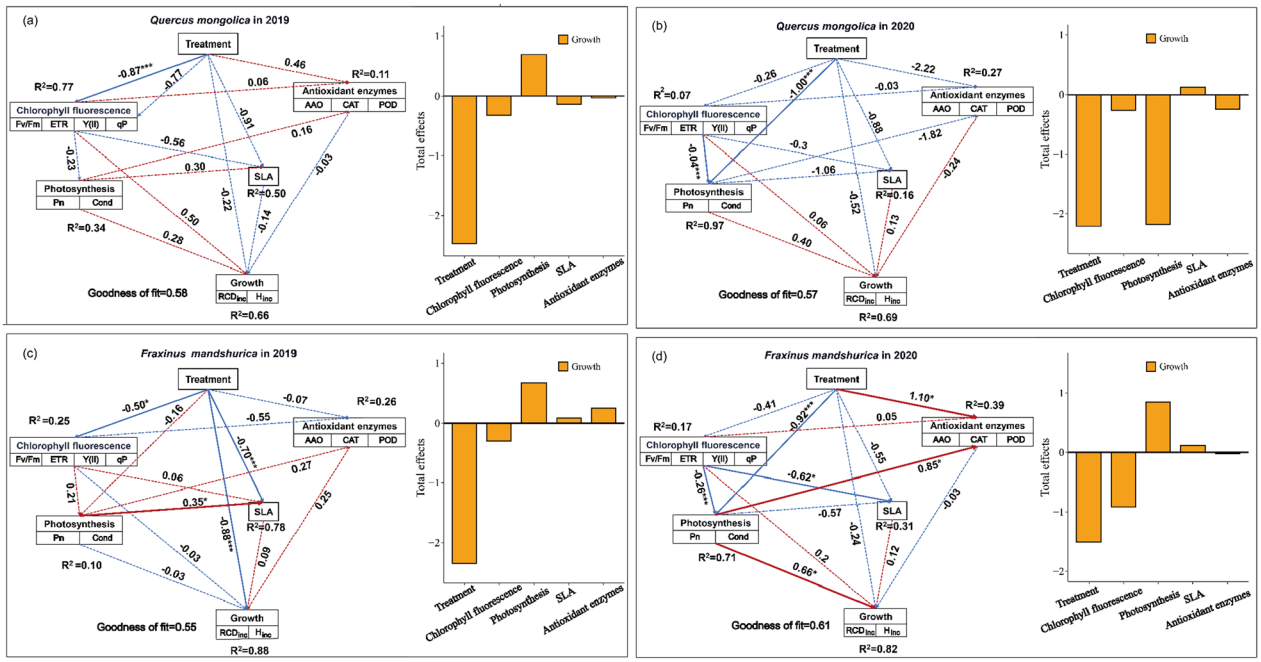


Fig. 7 Partial least squares path modeling (PLS-PM) for the effects of treatment, chlorophyll fluorescence, photosynthesis, specific leaf area (SLA) and antioxidant enzymes on growth and standardized total effects for *Q. mongolica* in 2019 (**a**, goodness of fit = 0.58) and 2020 (**b**, goodness of fit = 0.57) and *F. mandshurica* in 2019 (**c**, goodness of fit = 0.55) and 2020 (**d**, goodness of fit = 0.61). Chlorophyll fluorescence: maximum PSII quantum (F_v/F_m), electron transport rate (ETR), effective PSII quantum (Y(II)) and coefficient of photochemical quenching (qP); Antioxidant enzymes: ascorbate oxidase (AAO), catalase (CAT) and peroxidase (POD); Growth: the mean periodic increment in root collar diameter (RCD_{inc}) and mean periodic increment in height ($Height_{inc}$). Red lines represent positive paths; blue lines represent negative paths; the solid lines indicate significant correlation; the dotted lines indicate non-significant correlation; the values along the lines indicate the effect size; R^2 indicate the variance of dependent variable explained by the model. Significance levels of each symbol are $^{***}P \le 0.001$, $^{**}P \le 0.01$, and $^{*}P \le 0.05$

accumulation and the C/N of the leaves likely play important roles in mitigating oxidative damage in *F. mandshurica* seedlings.

Effects of warming on seedling growth in the drought year

Inter-annual variations in precipitation alter the effects of warming on the growth of seedlings, with pronounced impacts observed particularly in *F. mandshurica*. This finding supports previous studies indicating that drought adversely affects the response of carbon assimilation and growth to warming (Peñuelas et al. 2007; Deslauriers et al. 2014; Arain et al. 2022; Didion-Gency et al. 2022). In drought years, warming intensified the reduction in seedling growth increment in *F. mandshurica*, while having no significant effect on *Q. mongolica* (Fig. 1a–c). This finding partially supports the hypothesis (H2), which predicts that warming during drought years reduces photosynthesis and growth in both species, with a more pronounced decline anticipated in *F. mandshurica*. According to Cabon et al. (2022), under resource-limited conditions, tree growth is expected to be closely coupled with photosynthesis. Therefore, the growth reduction observed in *F. mandshurica* during drought years may be attributed to a decline in photosynthetic capacity (Fig. 7d) (Zhou et al. 2024). Therefore, ignoring interannual variations in precipitation may lead to an overestimation of carbon exchange in ecosystems (Rogers and Beringer 2017). Accounting for interannual variations in precipitation is essential for accurately estimating carbon exchange and for understanding ecosystem responses to warming. P_n is reduced under stress as a result of decreases in stomatal conductance, mesophyll conductance, and biochemical limitations (Carmo-Silva et al. 2012). Our results showed that warming decreased P_n, Cond, and photochemical quenching (qP) for two species. These findings suggest that reduced P_n may be driven by a combination of stomatal and non-stomatal restriction. Non-stomatal restriction may be attributed to reducing the activity of photosynthetic system II, Rubisco (e.g., Zheng et al. 2016; Liu et al. 2023), or anatomical changes (e.g., higher stomatal density, Hao et al. 2023). Further investigations into leaf anatomy, mesophyll conductance, and hydraulic properties are required to fully elucidate the effects of warming on the photosynthetic characteristics of *F. mandshurica* seedlings.

In our study, we observed contrasting patterns in leaf morphological traits across years with differing precipitation. In the year with normal precipitation, the reduced SLA and smaller leaf area (Fig. 2) suggest an investment in structurally robust, resource-efficient leaves, likely to enhance photosynthetic performance (Richards and Damschen 2022). Conversely, during drought year, the increase in SLA accompanied by reduced leaf area reflects a shift towards thinner, less costly leaves, representing a conservative strategy to minimize resource expenditure under stress. Although leaf thickness and leaf density were not measured in this study, the observed changes in SLA still provide valuable insights into the plant's physiological responses (Freschet et al. 2015; Tripathi et al. 2020). This demonstrates the species' morphological plasticity in response to varying environmental conditions. Moreover, the combined effects of warming and drought caused cellular membrane damage, as evidenced by increased MDA content, and led to reduced SOD and CAT activities in both species, whereas AAO and POD activities remained unaffected. Our findings demonstrate that different protective enzymes exhibit varying sensitivities to elevated temperatures (Du et al. 2024). The absence of significant warming effects on the growth of *Q. mongolica* seedlings (Fig. 1) indicates that this species is well adapted to future environmental conditions characterized by elevated temperatures and drought. This resilience may be attributed to its strong drought tolerance mechanisms, such as stomatal closure to reduce transpiration (Fig. 3; Fig. 6a) and the development of a deep and extensive root system (Yuan et al. 2022), which enables *Q. mongolica* to adapt effectively to drought conditions. However, further analysis of hydraulic traits (e.g., branch water conductivity, conduit width, leaf water potential) and soil water potential is necessary to elucidate the underlying mechanisms by which *Q. mongolica* responds to drought and warming. In addition, this study is limited to one drought-tolerant and one drought-intolerant species, which may restrict the generalizability of our findings to other species. Future studies should include a broader range of species with varying drought tolerances to better understand the ecological and physiological mechanisms and to assess the broader applicability of our results in the context of climate change. Furthermore, although seedlings are crucial for understanding initial growth and stress responses, their behavior may differ significantly from that of adult trees and may not accurately reflect the true carbon sequestration potential of adult trees.

Conclusion

Our study highlighted that a 2 °C increase in soil temperature tended to adversely impact the seedling growth of drought-intolerant species *F. mandshurica* seedlings. Moreover, the adverse effect of warming on the photosynthetic properties, antioxidant oxidase, and growth of *F. mandshurica* was reinforced in a drought year. These findings indicate that the effects of warming are species-specific, and drought-intolerant species *F. mandshurica* seedlings are more vulnerable to future global warming under drought conditions, compared to drought-tolerant species *Q. mongolica*.

Abbreviations

RCD_{inc}	Mean periodic increment in root collar diameter
$Height_{inc}$	Mean periodic increment in height
SLA	Specific leaf area
P_n	Net photosynthetic rate
T_r	Transpiration rate
Cond	Stomatal conductance
WUE	Water use efficiency
Ls	Stomatal limit value
F_v/F_m	Maximum PSII quantum
ETR	Electron transport rate
Y(II)	Effective PSII quantum
qP	Coefficient of photochemical quenching
MDA	Malondialdehyde
SOD	Superoxide dismutase
CAT	Catalase
POD	Peroxidase
AAO	Ascorbate oxidase
Leaf N	Leaf nitrogen
Leaf C/N	Ratio between leaf carbon and nitrogen

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13717-025-00645-6.

Additional file1.

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Author contributions

Junfeng Yuan analyzed the data and wrote the manuscript. Yunting Fang, Dongwei Liu, Lizhong Yu, Rongping Li, and Qiaoling Yan revised the manuscript. Shitong Gao, Aoyang Wang, and Junfeng Yuan contributed to data collection. Qiaoling Yan, Junfeng Yuan, Ting Zhang, and Yunting Fang designed the experiment. Qiaoling Yan, Rongping Li, and Junfeng Yuan provided financial support for the research. All authors have read and agreed to the published version of the manuscript.

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Availability of data and materials
The data that support the findings of this study are available from the corresponding authors upon reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
All authors approved the manuscript for publication in the Ecological Processes.

Competing interests
The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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