

Extreme warming and drought impair survival, physiological activity and adaptive root growth in *Pinus densiflora* seedlings

Jinseo Kim

Korea University

Heejae Jo

Korea University

Florent Noulèkoun

Korea University

Minyoung Kwon

Korea University

Hyung-sub Kim

Cornell University

Yowhan Son

yson@korea.ac.kr

Korea University

Research Article

Keywords: Climate change, Korean red pine, gas exchange, water-use efficiency, root biomass, biomass allocation

Posted Date: September 29th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10882586/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Abstract

Compound climate extremes, such as concurrent warming and drought, are projected to increase, yet their impacts on Korean conifer species remain poorly understood.

We investigated the individual and combined effects of extreme warming and drought on the survival, physiology and growth of *Pinus densiflora* Siebold & Zucc. seedlings in South Korea.

Three-year-old *P. densiflora* seedlings were exposed in an open-field experiment to extreme warming (+3.7 °C for 87 days), drought (100% precipitation exclusion for 33 days), and their combination. Survival, gas exchange, height, root-collar diameter, and biomass fractions were measured during and after treatment.

Extreme warming significantly reduced seedling survival, whereas drought did not. Both stressors independently reduced stomatal conductance, net photosynthesis, and transpiration, while water-use efficiency was maintained or increased; gas exchange recovered after treatments ceased. Neither warming nor drought significantly affected aboveground growth or biomass. In contrast, root biomass increased under individual warming or drought, but this compensatory response disappeared under combined warming and drought.

P. densiflora seedlings showed physiological resilience and adaptive root allocation under individual climate extremes, but compound warming and drought suppressed belowground compensation, potentially increasing vulnerability and constraining regeneration under future climate change.

Key message

Extreme warming and drought each promoted compensatory root investment in seedlings, but their combination reversed this response, indicating that compound climate stress constrains adaptive belowground allocation.

1. Introduction

The Intergovernmental Panel on Climate Change (IPCC) reported that the frequency and intensity of extreme climatic events, such as heatwaves and droughts, have significantly increased due to ongoing global climate change (IPCC, 2021). According to the Shared Socioeconomic Pathways (SSP) scenarios, extreme warming events in the mid-to-late 2000s are projected to become 5 to 20 times more frequent and intense compared to those recorded in the 1950s (IPCC, 2021). Moreover, altered precipitation patterns combined with increased evaporation rates are projected to amplify annual precipitation variability, leading to more frequent and severe droughts (IPCC, 2021; Ripple et al., 2023).

The increasing incidence of these extreme climate phenomena poses significant threats to the sustainability of terrestrial plant ecosystems (Arend et al., 2011; Penuelas et al., 2004). For instance,

extreme warming imposes severe heat stress on plants. Although warming might enhance photosynthesis and growth in cold, high-altitude ecosystems (Dusenge et al., 2023; Quan et al., 2024), it often decreases these physiological traits and negatively affects survival in temperate and tropical forest ecosystems (Adams et al., 2017; Frelich and Reich, 2010; Li et al., 2016). Moreover, elevated temperatures induce soil moisture loss and increase atmospheric water demand, thereby increasing vapor pressure deficit (VPD) (Balducci et al., 2015). Consequently, plants become increasingly susceptible to severe water stress (Adams et al., 2017). Similarly, extreme drought, resulting from erratic rainfall patterns and reduced annual precipitation, significantly reduces soil volumetric water content (VWC), thereby directly inhibiting plant physiological functions and growth (Anjum et al., 2017). Consequently, plants are compelled to activate a suite of acclimation and adaptation mechanisms to maintain functional stability under these rapidly changing environmental conditions.

In response to climate change, plants develop adaptive strategies involving physiological adjustments (Salvucci and Crafts-Brandner, 2004), growth pattern changes (Hatfield and Prueger, 2015) and modifications of biomass allocation and accumulation (Poorter et al., 2012). For example, plants adjust stomatal behavior by either increasing transpiration to dissipate heat or closing stomata to conserve water in response to drought (Farquhar and Sharkey, 1982). However, such adaptive responses can inadvertently increase the risk of dehydration or carbon starvation, ultimately compromising plant survival (Adams et al., 2017; Urban et al., 2017). Additionally, plants commonly optimize biomass allocation to above- or belowground components in response to environmental stressors, such as leaf area expansion under high temperatures and enhanced root development under low water availability (Poorter et al., 2012; Tumber-Dávila et al., 2022). Nonetheless, these adaptive strategies, while beneficial in the short term, may lead to reduced growth potential under improved environmental conditions or over longer time scales (Anderson and Song, 2020). Furthermore, cellular and tissue-level damage becomes more frequent under extreme stress conditions, substantially impairing plant competitive ability and survival rates (Ummenhofer and Meehl, 2017).

Notably, simultaneous exposure to heat and drought imposes more severe stress on plants than either condition alone, which can potentially exceed their adaptive capacity to sustain physiological function (Ummenhofer and Meehl, 2017). Concurrent warming and drought exacerbate soil moisture depletion (Naumann et al., 2018) and increase evapotranspiration, creating a feedback loop that further intensifies drought severity (Zhou et al., 2019). Higher soil temperatures accelerate water loss, thereby amplifying the severity of drought stress (Naumann et al., 2018). Under such conditions, plants face increasing physiological difficulty as they must balance water conservation and temperature regulation (Reich et al., 2018). If conditions persist, internal cellular water loss reduces specific heat capacity, diminishing turgor pressure and resulting in permanent tissue damage and reduced photosynthetic capability (Seleiman et al., 2021). Consequently, carbon-deficient plants may suffer impaired growth or mortality despite their efforts to adapt to climate change. Unfortunately, the frequency of concurrent extreme warming and drought events is projected to increase further, and the associated ecological impacts are expected to persist and intensify over the following decades (Ummenhofer and Meehl, 2017). Although compound

stress is a growing global concern, its impacts are expected to be particularly pronounced in regions such as East Asia, where climate variability and warming trends are accelerating.

East Asia is considered highly vulnerable to climate change due to its regional monsoon-driven rainfall patterns and rising average temperatures (Kim et al., 2021). Particularly in Korea, located within East Asia's temperate zone, an increased frequency of extreme warming and drought events has been reported (Kim et al., 2022), potentially leading to critical changes in forest ecosystems, most notably in coniferous forests. The proportion of coniferous forests in Korea has declined from approximately 48% of the total forest area in the 1990s to roughly 34% (Bhusal et al., 2020; Matyssek et al., 2014). Further reductions are anticipated if current climatic trends continue (Byun et al., 2010). Notably, severe coniferous tree mortality frequently observed in southern regions of Korea has been primarily attributed to severe drought stress induced by abnormal high-temperature events (Lee et al., 2004). Therefore, research investigating climate adaptation strategies, especially those targeting representative conifer species, is required to establish effective forest management practices.

Considering these trends, understanding plant adaptive strategies to combined effects of various extreme climatic stressors is critical for ensuring the long-term sustainability of forest ecosystems. It is essential not only to evaluate the immediate effects of extreme events but also to investigate their lasting impacts on plant survival and performance, as well as potential long-term consequences for ecosystem dynamics. Seedlings, in particular, represent the most vulnerable life stage, as their shallow roots and limited carbon reserves make them especially sensitive to climatic extremes (Niinemets, 2010).

This study aims to evaluate the effects of extreme warming and drought stress on *Pinus densiflora* Siebold & Zucc. seedlings which is a dominant conifer species in South Korea. We simulated projected temperature increase and water stress for the mid-2050s using infrared heating and automated rainout shelters, respectively, under open-field experiments. We specifically assessed how these extreme climatic events would affect the physiology and growth dynamics of three-year-old *P. densiflora* seedlings throughout the growing season (May to September 2022). We hypothesize that (1) the exposure of seedlings to either extreme warming or drought would reduce physiological activity and suppress growth and biomass accumulation, and (2) simultaneous exposure to both stressors would amplify physiological and growth-related impairments beyond the effects of individual treatments.

2. Material and methods

2.1. Study site

The study was conducted from March to November 2022 in an open-field nursery site at Korea University, Seoul, South Korea (37° 35'36"N, 127° 1'31"E). Seoul is located in a continental climate zone, where temperatures are highly variable, and precipitation is concentrated during the summer rainy season. According to the Korea Meteorological Administration (KMA, 2023), the mean annual

temperature of Seoul was 13.2°C in 2022. The annual precipitation was 1775.3 mm, of which 68.2% (1210.9 mm) was concentrated between June and August, 2022 (KMA, 2023).

Twenty experimental plots of 1.5 m² (1 m x 1.5 m) were established in the open-field nursery site on March 18, 2022 (Fig. 1a). The soil in each plot was excavated to a depth of 60 cm, thoroughly mixed to ensure homogeneity and then returned to each plot. To minimize interference among plots and prevent lateral water intrusion during precipitation manipulation, each plot was bordered with a rubber packing barrier installed to a depth of 30 cm below the ground surface. The soil was sandy loam (sand: 74.8%, silt: 16.1%, clay: 9.1%) with a pH of 5.67.

We planted twenty-eight (4 × 7) three-year-old *P. densiflora* seedlings per plot on March 20, 2022 (Fig. 1b). Prior to planting, the average height and root collar diameter (RCD) of the seedlings were 30.1 cm and 4.9 mm, respectively. Before planting, the roots of every seedling were trimmed to a length of 15 cm, following the Korea's national guidelines for seed and seedling management (KFS 2015).

2.2. Experimental design

To investigate the effects of future extreme climate events on *P. densiflora* seedlings, we designed our treatments based on projected climate scenarios for Korea for mid-21st century. We selected warming and drought as representative extreme climate events because they are already common in Korea and are expected to increase in both frequency and duration in the future. Extreme warming was simulated based on the maximum duration of warm days, and extreme drought was based on the maximum duration of consecutive dry days. Extreme warming consisted of two temperature levels (TC: control, TW: warming), and extreme drought consisted of two precipitation levels (PC: control, PD: drought). The resulting four treatment combinations included TC + PC (control), TC + PD (extreme drought), TW + TC (extreme warming) and TW + PD (combined warming and drought). The treatments were arranged in a fully factorial design and replicated five times using a randomized complete block design with each block including the four treatments (Fig. 2a).

The treatment duration and intensity were selected based on the SSP 5-8.5 scenario and the predictions of two Korean climate models (Jung and Lee, 2019; Kim et al., 2021). According to these models, the maximum duration of extreme warming and drought in Korea in mid-21st-century is projected to be 87 consecutive days and 33 days, respectively (Kim et al., 2021). The onset of extreme warming was estimated to occur on May 14 (Jung and Lee, 2019). Given the growing frequency and springtime concurrence of warming and drought in Korea (KEI, 2020; KMA 2022), both treatments were initiated on the same date, May 14. Accordingly, the extreme warming treatment was carried out by increasing the canopy temperature in TW plots by 3.7°C compared to TC plots for 87 days (i.e., from May 14 to August 10, 2022). The extreme drought treatment was carried out by blocking 100% precipitation in PD plots for 33 days (i.e., from May 14 to June 15, 2022).

We conducted our experiments in an open-field temperature and precipitation manipulation system (Kim et al., 2023). Two Infrared heaters (FT-1000, Mor Electronic Heating Assoc., USA) were installed 60 cm

above the seedling canopy on the TW plots (Fig. 2b). Dummy heaters were also placed in the TC plots to account for the shadow effect. Infrared thermometers (SI-111, Campbell Scientific Inc., USA) were installed 60 cm above the canopy of every plot to calculate the difference in canopy temperatures between the TC and TW plots every five minutes and automatically activate infrared heaters to compensate for the temperature difference.

The automatic rainout shelters (2.0 m length × 1.5 m width) were installed 1.6 m above the ground of the PD plots (Fig. 2b). The rainout shelters were kept folded until the rain detector (HTL-301, Haimil, Korea) sensed the raindrops to avoid differences in light intensity between the PC and PD plots. To measure the soil temperature and volumetric water content (VWC), a soil temperature moisture sensor (CS655, Campbell Scientific Inc., USA) was installed 10 cm underneath the soil surface of each plot. The data were collected every half-hour by data loggers (CR1000X, Campbell Scientific Inc., USA) and a relay system (SDM-CD16AC, Campbell Scientific Inc., USA).

2.3. Data collection

We collected several environmental data including canopy temperature, soil temperature, and VWC as daily averages for each corresponding day of year (DOY: 130–311, Fig. 3) and three treatment periods: Period 1 (concurrent temperature and precipitation manipulation), Period 2 (temperature-only manipulation), and Period 3 (post-manipulation, Supplementary Table S1).

We monitored the survival rate of *P. densiflora* seedlings once a month throughout the experiment. The leaf gas exchange rates were measured to quantify the physiological responses of *P. densiflora* seedlings to the treatments using a portable photosynthesis system (LI-6800, Li-COR Inc., USA). Leaf gas exchange measurements were conducted on cloudless, sunny days from 8:00 to 14:00. Measurements were taken at least three days after a rainy day to minimize measurement errors due to residual moisture on the leaves. From May to October 2022 measurements were performed six to eight times per month. During the measurements, the chamber (6 cm length × 6 cm width) environment of the portable photosynthesis system was maintained at constant conditions (flow: 700 $\mu\text{mol s}^{-1}$, fan speed: 10000 rpm, CO_2 concentration: 400 μmol , relative humidity: 60%, light intensity: 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Four needles (two pairs of leaves) from two randomly selected seedlings per plot were used for each measurement. Each pair was randomly selected from the middle of the stems that were newly developed in the experimental year.

The gas exchange rates, including net photosynthetic rate (A , $\mu\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$), transpiration rate (E , $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$), stomatal conductance (g_{sw} , $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$), and intercellular to ambient CO_2 concentration ratio (C_i/C_a) were calculated per unit leaf area. The leaf area was measured using a scanner (Perfection 4990, EPSON, Japan) and estimated using a leaf area calculator program (WinSEEDLE, Regents Inc., Canada). Instantaneous water use efficiency (WUE) and intrinsic water use efficiency ($iWUE$) were determined as A/E and A/g_{sw} , respectively.

The growth of seedlings was measured twice: two days before the treatments (May 12, 2022) and the day before the harvest (November 6, 2022). The height (cm) of every seedling was measured from the ground to the apical tip with a folding ruler. Likewise, every seedling's root collar diameter (RCD, cm) was measured 1.5 cm above the ground with a digital caliper (500101, Mitutoyo, Japan). The measurement results were used to estimate each seedling's height-to-RCD ratio ($H:D$, cm cm^{-1}).

Every seedling was harvested on November 7, 2022. Each harvested seedling was divided into three parts: leaf, stem, and root. Each part was oven-dried at 65°C for 48 hours and weighed for their respective biomass (g). The respective biomass was used to estimate the shoot-to-root ratio ($S:R$).

2.4. Statistical analysis

Two of the twenty plots (19th: TW + PC and 20th: TC + PC) were excluded from all subsequent analyses due to partial malfunctions in the open-field system. The data from the remaining plots were analyzed after removing outliers using the interquartile range (IQR) method.

The Kaplan–Meier analysis was used to evaluate seedling's survival over time (Kaplan and Meier, 1958; Noulèkoun et al., 2017). Survival curves under each treatment were estimated using the R package “survival” (Therneau, 2015). The differences in the survival curves between the treatments were tested using the log-rank test.

As most response variables exhibited non-normal distributions even after transformation, generalized linear mixed models (GLMM) were used to assess the effects of extreme warming, drought, and their interaction on seedling physiology (A , E , g_{sw} , $CiCa$, WUE , and $iWUE$) and growth (height, RCD, biomass, and $S:R$), using the R package “glmmTMB” (Brooks et al., 2017). Models were fitted using either the Gaussian (WUE , $iWUE$, leaf, root and total biomass) or Gamma family (g_{sw} , E , A , $CiCa$, stem biomass and $S:R$) with a log link, depending on the distributional characteristics of each response variable. To distinguish treatment effects during and after the experimental manipulation, separate models were fitted for the three treatment periods (Periods 1–3). For the physiological parameters, time of measurement and DOY were included as covariates to account for temporal variation. Plot ID was included as random effects to account for repeated measurements within plots. For height and RCD, initial values were included as covariates to account for baseline differences whereas individual tree ID was included as a random factor. For the biomass components, tree ID was also used as a random term in the GLMMs.

The significance of the fixed effects (warming or drought) and their interactions was evaluated using Type III analysis of variance (ANOVA) via the car package (Fox and Weisberg, 2018; Noulèkoun et al., 2025). The Tukey post-hoc test was employed to perform mean comparison in case of significant treatment effects. When significant interactions were detected, planned contrasts was conducted to evaluate the effect of warming within each precipitation level and vice versa, using the emmeans package (Lenth, 2023). Contrasts were tested without adjustment for multiple comparisons as they

represented a priori hypotheses about context-dependent treatment effects. All statistical analyses were performed using R version 4.5.1 (R Core Team, 2025).

3. Results

3.1. Survival responses to the extreme warming and drought treatments

Survival significantly differed among treatments (Fig. 4; log-rank $p = 0.017$). A reduction in seedling survival due to extreme warming was observed in June, with an average survival rate of 94.4% in the TW + PC plots, compared to 97.22% in TC + PC plots. By the end of the observation, October, survival declined to 90.08% on average in the TW plots, while the TC plots maintained a higher rate of 96.43% on average. In contrast, neither extreme drought nor its interaction with warming showed significant differences in survival rates in the TC + PD and TW + PD plots compared to the TC + PC plot (Supplementary Table S2).

3.2. Physiological responses to the extreme warming and drought treatments

There was no significant interaction between extreme warming and drought on gas exchange parameters of *P. densiflora* seedlings (Table 1, Fig. 5). However, individual treatment had a significant effect on gas exchange parameters during temperature and precipitation manipulation.

Extreme warming, during temperature manipulation (Periods 1 and 2), significantly decreased A , E , and g_{sw} in the TW + PC plots on average by 17.3%, 14.6%, and 15.0% in Period 1, and by 18.2%, 25.8%, and 27.2% in Period 2 compared to the TC + PC plots, respectively (Fig. 5a-c). In contrast, $CiCa$, WUE , and $iWUE$ were significantly affected by extreme warming only during Period 2. During Period 2, $CiCa$ in the TW + PC plots decreased on average by 6.7%, while WUE and $iWUE$ increased on average by 11.2% and 11.1% compared to the TC + PC plots, respectively (Fig. 5d-f).

Similarly, during Period 1, over the precipitation manipulation, extreme drought decreased A , E , and g_{sw} in the TC + PD plots on average by 20.1%, 23.5%, and 23.5% relative to the control plots, respectively. Despite the cessation of precipitation manipulation, the legacy effects of extreme drought were evident in Period 2. During Period 2, extreme drought decreased g_{sw} and $CiCa$ in TC + PD plots on average by 13.8% and 4.1% and increased $iWUE$ on average by 11.5% relative to the TC + PC plots, respectively (Fig. 5). By Period 3, when all manipulations concluded, the effects of extreme warming and drought were not significant.

Table 1

Summary of the results of Type III ANOVA performed on the generalized linear mixed-effects models (GLMMs) assessing the response of gas exchange parameters (*A*, *E*, *gsw*, *CiCa*, *WUE*, and *iWUE*) to extreme warming, drought, and their interaction, analyzed separately by temperature and precipitation manipulation periods. Significant effects ($p < 0.05$) are shown in bold. GLMMs were fitted for each period, with Time and DOY included as covariates and plot ID included as a random factor.

Factor	<i>A</i>			<i>E</i>			<i>gsw</i>		
	Period 1	Period 2	Period 3	Period 1	Period 2	Period 3	Period 1	Period 2	Period 3
TW	< 0.05	< 0.001	n.s	< 0.05	< 0.001	n.s	< 0.05	< 0.001	n.s
PD	< 0.05	n.s	n.s	< 0.01	n.s	n.s	< 0.01	< 0.05	n.s
TW×PD	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Time	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.05	< 0.001
DOY	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
	<i>CiCa</i>			<i>WUE</i>			<i>iWUE</i>		
	Period 1	Period 2	Period 3	Period 1	Period 2	Period 3	Period 1	Period 2	Period 3
TW	n.s	< 0.001	n.s	n.s	< 0.001	n.s	n.s	< 0.001	n.s
PD	n.s	< 0.05	n.s	n.s	n.s	n.s	n.s	< 0.05	n.s
TW×PD	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
Time	< 0.001	< 0.01	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.05	< 0.001
DOY	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

TW: extreme warming (TW + PC), PD: extreme drought (TC + PD), Time: time of measurement, DOY: day of the year, n.s.: not significant, *A*: net photosynthetic rate, *E*: transpiration rate, *gsw*: stomatal conductance, *CiCa*: intercellular to ambient CO₂ concentration ratio, *WUE*: Instantaneous water use efficiency, *iWUE*: intrinsic water use efficiency.

3.3. Growth responses to the extreme warming and drought treatments

Extreme warming and drought did not significantly affect the height or RCD of *P. densiflora* seedlings (Table 2, Fig. 6a, 6b). The analysis of the *H:R* revealed that height was strongly correlated with RCD

across the treatments (Fig. 6c). However, neither extreme warming nor drought influenced this relationship ($p > 0.05$).

Table 2

Summary of the results of Type III ANOVA performed on the generalized linear mixed-effects models (GLMMs) assessing the effects of extreme warming, drought, and their interaction on morphological parameters (height, RCD, and H:R) and biomass (leaf, stem, root, total, and shoot-to-root ratio [S:R]). Significant effects ($p < 0.05$) are shown in bold. GLMMs were fitted for growth and biomass variables, with tree ID included as a random factor. Initial height and RCD values were included as covariates in the models for height and RCD, respectively.

Factor	Growth parameters			Biomass				
	Height	RCD	H:R	Leaf	Stem	Root	Total	S:R
TW	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
PD	n.s	n.s	n.s	n.s	n.s	n.s	n.s	n.s
TW×PD	n.s	n.s	n.s	n.s	n.s	< 0.01	n.s	< 0.01
Initial height	< 0.001	NA	NA	NA	NA	NA	NA	NA
Initial RCD	n.s	< 0.001	NA	NA	NA	NA	NA	NA
TW: extreme warming (TW + PC); PD: extreme drought (TC + PD); NA: not applicable, n.s.: not significant								

Root biomass of *P. densiflora* seedlings showed a significant interaction effect between extreme warming and drought ($p < 0.01$; Table 2, Fig. 7a, 8a). Extreme warming increased root biomass under ambient precipitation (PC; +0.43 g, $p = 0.004$) but had no significant effect under extreme drought (PD; $p = 0.089$). Extreme drought increased root biomass under ambient temperature (TC; +0.36 g, $p = 0.025$) while decreasing it under extreme warming (TW; -0.33 g, $p = 0.020$). S:R also exhibited significant extreme warming and drought interaction ($p < 0.01$; Table 2, Fig. 7b, 8b). Extreme warming increased S:R only under extreme drought (PD; +0.30, $p = 0.001$) but not under ambient precipitation (PC; $p = 0.295$). Extreme drought decreased S:R under ambient temperature (TC; -0.29, $p = 0.002$) but not under extreme warming (TW; $p = 0.238$). In contrast, leaf and stem biomass showed no significant responses to warming, drought, or their interaction.

4. Discussion

4.1. Seedling survival was mainly affected by extreme warming

Our results partially supported our first hypothesis but contradicted the second hypothesis. We found that extreme warming in June (Period 1) was the primary driver of seedling mortality (Fig. 4). The absence of combined effects of warming and drought suggests that *P. densiflora* seedlings may possess sufficient drought tolerance capacity to withstand moderate water stress but lack comparable heat

tolerance mechanisms. Although both extreme warming and drought maintained similar VWC levels in the TW + PC and TC + PD plots during Period 1 (Supplementary Table S1, Fig. 3c), only extreme warming caused a significant decrease in survival. This suggests that heat stress, rather than water limitation, was the primary driver of mortality. Previous studies show that elevated temperatures can disrupt protein structure, enzyme activity, and membrane integrity, causing direct physiological damage not typically induced by drought alone (Bita and Gerats, 2013; Wahid et al., 2007). Our results suggest that *P. densiflora* seedlings likely possess considerable drought tolerance but that sudden and intense early-season warming may substantially reduce survival.

While reduced photosynthesis may also contribute to mortality, our findings do not support carbon starvation as a major cause. If carbon depletion was the main cause of mortality, we would expect mortality to continue or worsen throughout the temperature manipulation. Instead, survival declined abruptly in June and remained low or stable thereafter. Additionally, extreme drought treatments, which also suppress carbon assimilation, neither reduced survival (Fig. 4), nor the biomass (Fig. 7a) throughout the experiment. Given that carbon starvation typically requires prolonged exposure and precedes visible growth decline (McDowell and Sevanto, 2010), it is unlikely to have been the dominant driving mechanism of seedling mortality in our experiment.

4.2. Extreme warming and drought reduce physiological activities independently

Extreme warming and drought each exerted clear impacts on the physiological performance of *P. densiflora* seedlings, supporting our first hypothesis that exposure to either stressor would suppress gas exchange (Fig. 5a–f, Table 1). Both stressors induced rapid stomatal closure as evidenced by the reduced A , E and g_{sw} in response to warming and drought, consistent with the species' isohydric behavior, whereby stomata close promptly to prevent excessive water loss under declining water availability (Garcia-Forner et al., 2016; Matyssek et al., 2014). Previous studies on *P. densiflora* seedlings similarly report stomatal sensitivity to soil moisture depletion (An et al., 2022; Jo et al., 2025; Kim et al., 2024) reflecting a drought-tolerant strategy that maintains water status at the expense of carbon assimilation. In Period 1, reduced soil VWC in the extreme climatic treatments (Table S1, Fig. S2c) likely triggered stomatal down-regulation, allowing seedlings to maintain WUE and $iWUE$ at levels comparable to the control despite strong constraints on gas exchange (Fig. 5c-f).

During Period 2, when only warming was applied, physiological activity remained significantly reduced under the warming treatments. However, g_{sw} remained suppressed under drought even after precipitation manipulation ended. Soil VWC in TC + PD plots did not fully recover to control levels (Supplementary Table S1, Fig. 5c), and seedlings appeared to retain conservative stomatal behavior following prior water limitation. Such delays in stomatal reopening after drought relief have been attributed to persistent hydraulic constraints, including incomplete recovery of leaf hydraulic conductance (Knüver et al., 2025; Morabito et al., 2022). These mechanisms likely contributed to the lagged stomatal response observed in Period 2. Interestingly, g_{sw} also decreased under extreme

warming during Period 2, despite soil moisture being higher than during the warming phase of Period 1. Elevated temperatures increase atmospheric evaporative demand and leaf water loss, both of which promote stomatal closure independent of soil water availability (Grossiord et al., 2020; Oren et al., 1999). Moreover, stomatal responses to water stress are not always contingent to soil moisture availability, as high VPD during summer can induce stomatal closure even under adequate soil water availability (Novick et al., 2024). The reduced *gsw* under warming in Period 2 therefore, likely reflects an atmosphere-driven stomatal response to extreme temperature and VPD conditions.

Seasonal progression substantially influenced physiological responses. Across treatments, *A* and *E* increased in Period 2 relative to Period 1 (Fig. 5a–b), consistent with seasonal enhancement of conifer photosynthetic capacity during needle maturation (Warren, 2006). Period 2 coincides with the period when *P. densiflora* needles reach full maturity (Jo et al., 2019). However, under extreme warming, reductions in *gsw* and *E* during Period 2 were more than twice those observed in Period 1, indicating that heat stress coupled with high summer temperatures can override expected seasonal acclimation. This aligns with previous findings that extreme warming imposed on high temperature background conditions disproportionately constrain gas exchange in *P. densiflora* seedling (Jo et al., 2025).

Despite large declines in *gsw* and *E*, the reduction in *A* under extreme warming remained modest. This decoupling suggests that photosynthesis was partially maintained by non-stomatal processes, likely through thermal stimulation of biochemical reactions such as Rubisco activation and RuBP regeneration (Farquhar and Sharkey, 1982). Many conifers exhibit peak Rubisco activation near 35°C (Crous et al., 2022), implying that high temperatures may partially enhance biochemical capacity even under reduced stomatal conductance. This result is consistent with a previous finding which reported that plants can adjust their internal biochemical pathways to enhance carbon fixation efficiency even when stomatal conductance is low (Yi et al., 2019). Consequently, the disproportionate decline in *gsw* relative to *A* in response to warming likely increased intrinsic water-use efficiency (*WUE* and *iWUE*), while simultaneously reducing the *CiCa*, as observed in TW + PC plots during Period 2 (Fig. 5d–f). This demonstrates the ability of *P. densiflora* seedlings to adapt to warming through physiological adjustments.

Plants experiencing severe temperature or drought stress often require extended recovery periods or may suffer irreversible damage to their photosynthetic apparatus (Saxe et al., 2001). However, during Period 3, we observed a recovery of net photosynthetic rate and related physiological parameters following the cessation of temperature and precipitation manipulation. This observation suggests that the imposed stress levels might be relatively mild for the species, despite being classified as extreme based on future projections. This is corroborated by previous findings showing that mild stress induces temporary declines in gas exchange, followed by rapid recovery once the stressor is removed (Ruehr et al., 2019). Alternatively, it could be that the species possesses a high recovery capacity. In this regard, similar patterns of rapid post-stress recovery have been reported across multiple species, including *Pinus taeda* L. (Ameye et al., 2012), *Vitis amurensis* Rupr. (Luo et al., 2011), *P. densiflora* (Jo et al., 2019; Jo et al., 2025), *Larix kaempferi* Lamb. (An et al., 2022; Kim et al., 2024), and *Abies holophylla* Maxim. (Jo

et al., 2022). This adaptive capacity prevented the amplified stress responses that would have resulted in synergistic interactions, demonstrating the high resilience of this drought-tolerant species to extreme climate stress conditions in a short term.

4.3 Extreme warming and drought, both independently and interactively, influence biomass accumulation and allocation but not seedling growth

Extreme climatic events often alter growth trajectories and biomass partitioning in woody species (Tumber-Dávila et al., 2022; Umaña et al., 2021). We hypothesized that extreme warming and drought would reduce overall growth. However, neither the individual treatments nor their interaction significantly affected aboveground biomass, despite the observed reductions in net photosynthetic rates in response to the treatments (Table 2, Fig. 6a). Two mechanisms can explain this apparent decoupling between physiological and structural responses.

First, *P. densiflora* is a fixed-growth species whose current-year leaf and shoot production is largely predetermined by leaf primordia formed during the previous growing season (Jo et al., 2019; Tsukahara et al., 1985). Thus, aboveground growth in the treatment year depends more on prior-year resource acquisition than on concurrent environmental conditions. Such decoupling is consistent with evidence that conifer seedlings maintain new shoot growth by mobilizing internal reserves even when photosynthesis is reduced (Ji et al., 2021; Woodruff and Meinzer, 2011). Similar reliance on nonstructural carbohydrate (NSC) pools during drought has been documented in *Pinus sylvestris* L., enabling seedlings to maintain growth and survival under restricted carbon assimilation (Galiano et al., 2011). Second, the stress duration in our experiment may have been insufficient to alter aboveground structural development. Many conifers exhibit lagged growth responses to heat and drought, whereby growth suppression becomes evident only in subsequent seasons (Anderegg et al., 2015; Babst et al., 2014). Thus, although photosynthetic activity declined, the growing season of *P. densiflora* which extends from March through September, may have allowed seedlings to compensate once stress abated. Overall, our result suggests that either nutrient availability remained adequate throughout the season or that seedlings exhibited compensatory growth after the treatments ended (Poorter et al., 2012).

In contrast to aboveground growth, belowground biomass allocation exhibited significant responses to extreme warming and drought interactions (Table 2, Fig. 8a). Under single stressors, both extreme warming and extreme drought increased root biomass, but only when the other environmental factor remained non-limiting. Under ambient precipitation, extreme warming increased root biomass, likely reflecting increased evaporative demand and the need to enhance water uptake capacity. Likewise, under ambient temperature, extreme drought stimulated compensatory root growth, consistent with well-documented drought-avoidance strategies in woody plants (Brunner et al., 2015; Padilla and Pugnaire, 2007; Umaña et al., 2021). Soil moisture patterns during our experiment support this interpretation. Soil VWC was significantly lower in both TW + PC and TC + PD plots relative to TC + PC during the treatment manipulation (Supplementary Table S1), indicating increased physiological water use under the treatments. Enhanced root growth under these individual stressors reflects a compensatory plant

strategy to maintain water balance. When warming and drought co-occurred, root responses fundamentally shifted. Under reduced precipitation, extreme warming no longer enhanced root biomass. This aligns with experimental evidence showing that soil moisture acts as a primary limiting factor that constrains warming-induced increases in fine root production in *P. densiflora* seedlings (Han et al., 2017). In drying soil, declining hydraulic conductivity and drought-induced hormonal signals restrict carbon allocation to root growth, causing warming-induced increases in root production to collapse once moisture availability falls below a physiological threshold (Davies and Zhang, 1991).

More importantly, the drought-induced increase in root biomass reversed under elevated temperature. In the TW + PD plot, root biomass declined. This pattern indicates that combined warming and drought exceeded seedlings' physiological thresholds, transitioning the response from compensatory growth to stress-induced root impairment. Elevated temperature increases evapotranspiration and accelerates soil water depletion, while drought-induced stomatal closure reduces transpirational cooling, amplifying tissue heating (Farquhar and Sharkey, 1982; Prasad et al., 2008; Zhou et al., 2019). Reduced soil moisture also decreases soil specific heat capacity, causing soils to warm more rapidly and potentially exposing roots to damaging thermal loads (Haj Sghaier et al., 2022). Under such conditions, severe dehydration diminishes cellular thermal buffering and increases susceptibility to irreversible damage (Seleiman et al., 2021). This is consistent with previous findings where severe moisture deficits disrupted carbon transport between shoots and roots in *Pinus flexilis* E., impairing root function and survival (Reinhardt et al., 2015). Consistent with this mechanism, the TW + PD plot exhibited both the highest soil temperatures and the lowest VWC during Period 1 (Supplementary Table S1). The elevated VWC observed in Periods 2–3 may partly reflect reduced root water uptake capacity rather than solely improved soil moisture, suggesting partial impairment of root function under compound stress. Given the vulnerability of juvenile root tissues (Niinemets, 2010), the combined stresses likely led to root suppression rather than compensation.

S:R responses closely paralleled root biomass patterns (Table 2, Fig. 7b, 8b). Under ambient temperature, drought decreased S:R, indicating drought-induced increases in biomass allocation to root (Poorter et al., 2012). However, this adaptive allocation disappeared under elevated temperature, supporting the evidence that warming intensified drought-related stress and constrained root function. Under ambient precipitation, extreme warming did not significantly alter S:R, even though root biomass increased. This likely reflects proportional whole-plant growth rather than selective reallocation. In contrast, under reduced precipitation, extreme warming increased S:R, driven primarily by a decline in root biomass under combined extreme warming and drought. This pattern suggests that seedlings abandoned further investment in compromised roots and instead allocated resources toward maintaining aboveground structures, potentially to preserve future recovery capacity.

The stability of aboveground biomass across treatments, even when photosynthesis was lowest in the TW + PD (Fig. 6), further supports a compensatory mechanism such as mobilization of NSCs (Galiano et al., 2011) or fixed-growth (Jo et al., 2019) constraints that decouple aboveground production from current carbon assimilation. Together, these findings indicate a hierarchical stress response: moderate

single-factor stresses promote compensatory root growth, whereas severe co-occurring stresses induce a switch toward survival-oriented allocation patterns, consistent with the stress-threshold framework proposed by Ruehr et al. (Ruehr et al., 2019).

Although immediate aboveground morphological responses were limited, belowground impairment may have important long-term consequences. Several studies have shown that drought- or heat-induced physiological disruptions can suppress growth for multiple subsequent years (Anderegg et al., 2015; Babst et al., 2014). Repeated or closely spaced extreme events may prevent root-system recovery, creating cumulative legacy effects that progressively erode stress tolerance. Given projections of increasingly frequent concurrent warming and drought (Ummenhofer and Meehl, 2017), this shift from compensatory root proliferation under single stressors to root growth suppression under compound stress highlights a critical risk for *P. densiflora* regeneration. Multi-year monitoring of belowground function will be essential to determine whether seedlings can recover or whether compound extremes impose lasting limits on forest regeneration potential.

5. Conclusion

This study examined how extreme climatic conditions influence the survival, physiological activity, and biomass accumulation and allocation of *P. densiflora* seedlings. Extreme warming significantly reduced survival during the early growth stage. Both extreme warming and drought suppressed stomatal conductance, thereby reducing photosynthesis and transpiration while maintaining water-use efficiency. However, these physiological responses were decoupled from aboveground biomass accumulation, as none of the aboveground biomass fractions responded significantly to the treatments. In contrast, root biomass and biomass allocation were affected by the treatments. Each stressor individually promoted compensatory increases in root biomass under non-limiting conditions, whereas this response was reversed under concurrent exposure to both stressors. The combination of extreme warming and drought suppressed biomass allocation, suggesting that compound stress exceeded physiological tolerance thresholds and impaired root function. These findings indicate that although *P. densiflora* seedlings exhibit physiological resilience to individual stressors, their capacity to concurrent climate extremes may be constrained by the loss of adaptive root allocation, which could reduce water uptake capacity and compromise recovery during future stress events. However, because this study was conducted over a single growing season, the observed physiological recovery and shifts in biomass allocation may not fully capture the longer-term legacy effects of extreme warming and drought. Therefore, longer-term assessments are needed to determine whether the observed suppression of adaptive root allocation persists, recovers, or intensifies under repeated or prolonged compound climate stress.

Declarations

- **Funding**

This research was supported by the Core Research Institute Basic Science Research Program provided by the National Research Foundation of Korea (NRF) funded by the Ministry of Education (NRF-2021R1A6A1A10045235); the Carbon Neutral Infrastructure Building Program provided by the Korea Forestry Promotion Institute (KoFPI) (RS-2022-KF002024; RS-2024-00403486)

- **Competing Interests**

The authors have no relevant financial or non-financial interests to disclose.

- **Author contributions**

Conceptualization was carried out by Jinseo Kim, Minyoung Kwon and Yowhan Son. Methodology was developed by Jinseo Kim, Heejae Jo and Minyoung Kwon. Formal analysis and investigation were performed by Jinseo Kim, Heejae Jo and Minyoung Kwon. The first draft of the manuscript was written by Jinseo Kim, and Heejae Jo, Florent Noulèkoun, Hyung-sub Kim and Yowhan Son commented on previous versions of the manuscript. Funding acquisition, resources and supervision were provided by Yowhan Son. All authors read and approved the final manuscript.

- **Data Availability**

The datasets generated during the current study are available from the corresponding author on reasonable request.

- **Acknowledgements**

The authors thank Korea University and the members of the ecosystem ecology laboratory for their assistance.

- **Conflicts of interest/Competing interests**

The authors declare no conflicts of interest.

- **Consent for publication**

All authors gave their informed consent to this publication and its content.

References

1. Adams HD, Barron-Gafford GA, Minor RL, Gardea AA, Bentley LP, Law DJ, Breshears DD, McDowell NG, Huxman TE (2017) Temperature response surfaces for mortality risk of tree species with future drought. *Environ Res Lett* 12:115014. doi.org/10.1088/1748-9326/aa93be
2. Ameye M, Wertin TM, Bauweraerts I, McGuire MA, Teskey RO, Steppe K (2012) The effect of induced heat waves on *Pinus taeda* and *Quercus rubra* seedlings in ambient and elevated CO₂ atmospheres. *New Phytol* 196:448–461. doi.org/10.1111/j.1469-8137.2012.04267.x

3. An J, Chang H, Han SH, Khamzina A, Son Y (2022) Differential water-use and growth responses of *Pinus densiflora* and *Larix kaempferi* seedlings to microclimate manipulation. *Turkish J Agric Forestry* 46:466–476. doi.org/10.55730/1300-011X.3018
4. Anderegg WR, Schwalm C, Biondi F, Camarero JJ, Koch G, Litvak M, Ogle K, Shaw JD, Shevliakova E, Williams A (2015) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* 349:528–532. doi.org/10.1126/science.aab1833
5. Anderson JT, Song BH (2020) Plant adaptation to climate change—Where are we? *J Syst Evol* 58:533–545. doi.org/10.1111/jse.12649
6. Anjum SA, Ashraf U, Zohaib A, Tanveer M, Naeem M, Ali I, Tabassum T, Nazir U (2017) Growth and developmental responses of crop plants under drought stress: a review. *Zemdirbyste-Agriculture* 104. doi.org/10.13080/z-a.2017.104.034
7. Arend M, Kuster T, Günthardt-Goerg MS, Dobbertin M (2011) Provenance-specific growth responses to drought and air warming in three European oak species (*Quercus robur*, *Q. petraea* and *Q. pubescens*). *Tree Physiol* 31:287–297. doi.org/10.1093/treephys/tpr004
8. Babst F, Alexander MR, Szejner P, Bouriaud O, Klesse S, Roden J, Ciais P, Poulter B, Frank D, Moore DJ (2014) A tree-ring perspective on the terrestrial carbon cycle. *Oecologia* 176:307–322. doi.org/10.1007/s00442-014-3031-6
9. Balducci L, Deslauriers A, Giovannelli A, Beaulieu M, Delzon S, Rossi S, Rathgeber CB (2015) How do drought and warming influence survival and wood traits of *Picea mariana* saplings? *J Exp Bot* 66:377–389. doi.org/10.1093/jxb/eru431
10. Bhusal N, Lee M, Han AR, Han A, Kim HS (2020) Responses to drought stress in *Prunus sargentii* and *Larix kaempferi* seedlings using morphological and physiological parameters. *For Ecol Manag* 465. doi.org/10.1016/j.foreco.2020.118099
11. Bitá CE, Gerats T (2013) Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. *Front Plant Sci* 4:273. doi.org/10.3389/fpls.2013.00273
12. Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400. doi.org/10.32614/RJ-2017-066
13. Brunner I, Herzog C, Dawes MA, Arend M, Sperisen C (2015) How tree roots respond to drought. *Front Plant Sci* 6:547. doi.org/10.3389/fpls.2015.00547
14. Byun J-G, Lee W-K, Choi J-K, Lee Y-J, Chung D-J (2010) Spatial distribution change of forest cover by climate change in Korea. *Proceeding of 2010 ESRI International User Conference, San Diego, CA*
15. Crous KY, Uddling J, De Kauwe MG (2022) Temperature responses of photosynthesis and respiration in evergreen trees from boreal to tropical latitudes. *New Phytol* 234:353–374. doi.org/10.1111/nph.17951
16. Davies WJ, Zhang J (1991) Root signals and the regulation of growth and development of plants in drying soil. *Annu Rev Plant Biol* 42:55–76. doi.org/10.1146/annurev.pp.42.060191.000415

17. Dusenge ME, Warren JM, Reich PB, Ward EJ, Murphy BK, Stefanski A, Bermudez R, Cruz M, McLennan DA, King AW (2023) Boreal conifers maintain carbon uptake with warming despite failure to track optimal temperatures. *Nat Commun* 14:4667. doi.org/10.1038/s41467-023-40248-3
18. Farquhar GD, TD Sharkey (1982) Stomatal conductance and photosynthesis. *Annu Rev Plant Physiol* 33:317–345. doi.org/10.1146/annurev.pp.33.060182.001533
19. Fox J (2018) *S Weisberg An R companion to applied regression*, Sage publications
20. Frelich LE, Reich PB (2010) Will environmental changes reinforce the impact of global warming on the prairie–forest border of central North America? *Front Ecol Environ* 8:371–378. doi.org/10.1890/080191
21. Galiano L, Martínez-Vilalta J, Lloret F (2011) Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 year after a drought episode. *New Phytol* 190:750–759. doi.org/10.1111/j.1469-8137.2010.03628.x
22. Garcia-Forner N, Adams HD, Sevanto S, Collins AD, Dickman LT, Hudson PJ, Zeppel MJ, Jenkins MW, Powers H, J Martínez-Vilalta (2016) Responses of two semiarid conifer tree species to reduced precipitation and warming reveal new perspectives for stomatal regulation. *Plant Cell Environ* 39:38–49. doi.org/10.1111/pce.12588
23. Grossiord C, Buckley TN, Cernusak LA, Novick KA, Poulter B, Siegwolf RT, Sperry JS, NG McDowell (2020) Plant responses to rising vapor pressure deficit. *New Phytol* 226:1550–1566. doi.org/10.1111/nph.16485
24. Haj Sghaier A, Tarnawa Á, Khaeim H, Kovács GP, Gyuricza C, Kende Z (2022) The effects of temperature and water on the seed germination and seedling development of rapeseed (*Brassica napus* L). *Plants* 11:2819. doi.org/10.3390/plants11212819
25. Han SH, Kim S, Li G, Chang H, Yun SJ, An J, Son Y (2017) Effects of warming and precipitation manipulation on fine root dynamics of *Pinus densiflora* Sieb. et Zucc seedlings *Forests* 9:14. doi.org/10.3390/f9010014
26. Hatfield JL, Prueger JH (2015) Temperature extremes: Effect on plant growth and development. *Weather Clim Extremes* 10:4–10. doi.org/10.1016/j.wace.2015.08.001
27. IPCC (2021) *Climate change 2021: the physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, p 2391
28. Ji L, Liu Y, Wang J, Lu Z, Zhang L, Yang Y (2021) Differential variation in non-structural carbohydrates in root branch orders of *Fraxinus mandshurica* Rupr. Seedlings Across different drought intensities and soil substrates. *Front Plant Sci* 12:692715. doi.org/10.3389/fpls.2021.692715
29. Jo H, Chang H, Han SH, An J, Yang AR, Y Son (2019) Abnormal Shoot Responses of *Pinus densiflora* Seedlings to Open-field Experimental Warming and Precipitation Manipulation. *J Clim Change Res* 10:1–8. doi.org/10.15531/kscrr.2019.10.1.1
30. Jo H, Noulèkoun F, Khamzina A, Chang H, Son Y (2022) Physiological and shoot growth responses of *Abies holophylla* and *Abies koreana* seedlings to open-field experimental warming and increased

- precipitation. *Water* 14:356. doi.org/10.3390/w14030356
31. Jo H, Noulèkoun F, Yi K, Kim J, Kim G-J, Kwon M, Kim G, Lee J-A, Lee J-M, Son Y (2025) Gas exchange of *Pinus densiflora* seedlings is reduced by the combined effect of high summer temperatures and cumulative heat under open-field warming. *Tree Physiol* 45:tpaf064. doi.org/10.1093/treephys/tpaf064
 32. Jung E, Lee S (2019) Study on the Onset Date and End Date Changes of Extreme Temperature Events in South Korea. *J Clim Res* 14:53–68. 10.14383/cri.2019.14.2.53
 33. Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. *J Am Stat Assoc* 53:457–481. doi.org/10.1080/01621459.1958.10501452
 34. KEI (2020) Korea Climate Change Assessment Report 2020: Climate Change Science. Korea Environment Institute, Sejong
 35. KFS (2015) Guidelines for Seed and Seedling Management. Daejeon, Korea, Korea Forest Service
 36. Kim D-H, Kim J-U, Byun Y-H, Kim T-J, Kim J-WK, Kim Y-HK, Ahn J-B, Cha D-H, Min S-K, Chang E-C (2021) Future Projection of Extreme Climate over the Korean Peninsula Using Multi-RCM in CORDEX-EA Phase 2 Project. *Atmosphere* 31:607–623. doi.org/10.14191/Atmos.2021.31.5.607
 37. Kim G-J, Jo H, Cho MS, Noh NJ, Han SH, Khamzina A, Kim H-S, Son Y (2024) Photosynthetic responses of *Larix kaempferi* and *Pinus densiflora* seedlings are affected by summer extreme heat rather than by extreme precipitation. *Sci Rep* 14:5250. doi.org/10.1038/s41598-024-56120-3
 38. Kim G-J, Jo H, Kim H, Cho M, Noh N, Chang H, Kim H-S, Son Y (2023) Experimental design of open-field temperature and precipitation manipulation system to simulate summer extreme climate events for plants and soils. *Turkish J Agric Forestry* 47:132–142. doi.org/10.55730/1300-011X.3070
 39. Kim K, Woo S, Baek E, Jeong J (2022) Characteristics of and changes in summertime flash droughts in South Korea, 1982 ~ 2020. *J Clim Change Res* 13:283–298. doi.org/10.15531/KSCCR.2022.13.3.283
 40. KMA (2022) Annual Report on Abnormal Climate of 2021. Seoul, Korea, Korea Meteorological Administration
 41. KMA (2023) Korea Meteorological Administration climate information portal. Climate statistical analysis: Temperature. (KR) <https://data.kma.go.kr/stcs/grnd/grndTaList.do>. (15 May 2025, date last accessed)
 42. KMA (2023) Korea Meteorological Administration climate information portal. Climate statistical analysis: Precipitation. (KR) <https://data.kma.go.kr/stcs/grnd/grndRnList.do?pgmNo=69>. (15 May 2025, date last accessed)
 43. Knüver T, Bär A, Hamann E, Zuber M, Mayr S, Beikircher B, Ruehr NK (2025) Stress dose explains drought recovery in *Norway spruce*. *Front Plant Sci* 16:1542301. doi.org/10.3389/fpls.2025.1542301
 44. Lee CS, Kim JH, Yi H, You YH (2004) Seedling establishment and regeneration of Korean red pine (*Pinus densiflora* S. et Z.) forests in Korea in relation to soil moisture. *For Ecol Manag* 199:423–432. doi.org/10.1016/j.foreco.2004.05.053

45. Lenth R (2023) emmeans: Estimated Marginal Means, aka Least-Squares Means_. R package version 18:5
46. Li Y, Liu J, Zhou G, Huang W, Duan H (2016) Warming effects on photosynthesis of subtropical tree species: a translocation experiment along an altitudinal gradient. *Sci Rep* 6:24895. doi.org/10.1038/srep24895
47. Luo H-B, Ma L, Xi H-F, Duan W, Li S-H, Loescher W, Wang J-F, Wang L-J (2011) Photosynthetic responses to heat treatments at different temperatures and following recovery in grapevine (*Vitis amurensis* L.) leaves. *PLoS ONE* 6:e23033. doi.org/10.1371/journal.pone.0023033
48. Matyssek R, Kozovits AR, Wieser G, Augustaitiene I, Augustaitis A (2014) Biological reactions of forests to climate change and air pollution. Springer, pp 671–673. doi.org/10.1007/s10342-014-0803-9
49. McDowell NG, Sevanto S (2010) The mechanisms of carbon starvation: how, when, or does it even occur at all? *New Phytol* 186:264–266. doi.org/10.1111/j.1469-8137.2010.03232.x
50. Morabito C, Orozco J, Tonel G, Cavalletto S, Meloni GR, Schubert A, Gullino ML, Zwieniecki MA, Secchi F (2022) Do the ends justify the means? Impact of drought progression rate on stress response and recovery in *Vitis vinifera*. *Physiol Plant* 174:e13590. doi.org/10.1111/ppl.13590
51. Naumann G, Alfieri L, Wyser K, Mentaschi L, Betts RA, Carrao H, Spinoni J, Vogt J, Feyen L (2018) Global changes in drought conditions under different levels of warming. *Geophys Res Lett* 45:3285–3296. doi.org/10.1002/2017GL076521
52. Niinemets Ü (2010) Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *For Ecol Manag* 260:1623–1639. doi.org/10.1016/j.foreco.2010.07.054
53. Noulèkoun F, Lamers JP, Naab J, Khamzina A (2017) Shoot and root responses of woody species to silvicultural management for afforestation of degraded croplands in the Sudano-Sahelian zone of Benin. *For Ecol Manag* 385:254–263. doi.org/10.1016/j.foreco.2016.11.018
54. Noulèkoun F, Mensah S, Kim H, Houndonougbo JSH, Mensah M, Lee WK, Son Y, Khamzina A (2025) Contrasting ecological mechanisms mediate the impact of land conversion on ecosystem multifunctionality. *Funct Ecol* 39:783–798. doi.org/10.1111/1365-2435.14738
55. Novick KA, Ficklin DL, Grossiord C, Konings AG, Martínez-Vilalta J, Sadok W, Trugman AT, Williams AP, Wright AJ, Abatzoglou JT (2024) The impacts of rising vapour pressure deficit in natural and managed ecosystems. *Plant Cell Environ* 47:3561–3589. doi.org/10.1111/pce.14846
56. Oren R, Sperry J, Katul G, Pataki D, Ewers B, Phillips N, K Schäfer (1999) Survey and synthesis of intra-and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant Cell Environ* 22:1515–1526. doi.org/10.1046/j.1365-3040.1999.00513.x
57. Padilla F, Pugnaire F (2007) Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. *Funct Ecol* doi.org/10.1111/j.1365-2435.2007.01267.x:489-495. doi.org/10.1111/j.1365-2435.2007.01267.x

58. Penuelas J, Gordon C, Llorens L, Nielsen T, Tietema A, Beier C, Bruna P, Emmett B, Estiarte M, Gorissen A (2004) Nonintrusive field experiments show different plant responses to warming and drought among sites, seasons, and species in a north–south European gradient. *Ecosystems* 7:598–612. doi.org/10.1007/s10021-004-0179-7
59. Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol* 193:30–50. doi.org/10.1111/j.1469-8137.2011.03952.x
60. Prasad P, Staggenborg S, Ristic Z (2008) Impacts of drought and/or heat stress on physiological, developmental, growth, and yield processes of crop plants. *Response of crops to limited water: Understanding and modeling water stress effects on plant growth processes* 1:301–355. doi.org/10.2134/advagricsystmodel1.c11
61. Quan Q, He N, Zhang R, Wang J, Luo Y, Ma F, Pan J, Wang R, Liu C, Zhang J (2024) Plant height as an indicator for alpine carbon sequestration and ecosystem response to warming. *Nat Plants* 10:890–900. doi.org/10.1038/s41477-024-01705-z
62. Reich PB, Sendall KM, Stefanski A, Rich RL, Hobbie SE, Montgomery RA (2018) Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. *Nature* 562:263–267. doi.org/10.1038/s41586-018-0582-4
63. Reinhardt K, Germino MJ, Kueppers LM, Domec J-C, Mitton J (2015) Linking carbon and water relations to drought-induced mortality in *Pinus flexilis* seedlings. *Tree Physiol* 35:771–782. doi.org/10.1093/treephys/tpv045
64. Ripple WJ, Wolf C, Gregg JW, Rockström J, Newsome TM, Law BE, Marques L, Lenton TM, Xu C, Huq S (2023) The 2023 state of the climate report: Entering uncharted territory. *Bioscience* 73:841–850. doi.org/10.1093/biosci/biad080
65. Ruehr NK, Grote R, Mayr S, Arneth A (2019) Beyond the extreme: recovery of carbon and water relations in woody plants following heat and drought stress. *Tree Physiol* 39:1285–1299. doi.org/10.1093/treephys/tpz032
66. Salvucci ME, Crafts-Brandner SJ (2004) Inhibition of photosynthesis by heat stress: the activation state of Rubisco as a limiting factor in photosynthesis. *Physiol Plant* 120:179–186. doi.org/10.1111/j.0031-9317.2004.0173.x
67. Saxe H, Cannell MG, Johnsen Ø, Ryan MG, Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytol* 149:369–399. doi.org/10.1046/j.1469-8137.2001.00057.x
68. Seleiman MF, Al-Suhaibani N, Ali N, Akmal M, Alotaibi M, Refay Y, Dindaroglu T, Abdul-Wajid HH, Battaglia ML (2021) Drought stress impacts on plants and different approaches to alleviate its adverse effects. *Plants* 10:259. doi.org/10.3390/plants10020259
69. Therneau T (2015) A package for survival analysis in S. R package version 2:2014
70. Tsukahara H, Kozłowski T, Shanklin J (1985) Tolerance of *Pinus densiflora*, *Pinus thunbergii*, and *Larix leptolepis* seedlings to SO₂. *Plant and soil* 88:385–397. doi.org/10.1007/bf02197495

71. Tumber-Dávila SJ, Schenk HJ, Du E, Jackson RB (2022) Plant sizes and shapes above and belowground and their interactions with climate. *New Phytol* 235:1032–1056.
doi.org/10.1111/nph.18031
72. Umaña MN, Cao M, Lin L, Swenson NG, Zhang C (2021) Trade-offs in above-and below-ground biomass allocation influencing seedling growth in a tropical forest. *J Ecol* 109:1184–1193.
doi.org/10.1111/1365-2745.13543
73. Ummenhofer CC, Meehl GA (2017) Extreme weather and climate events with ecological relevance: a review. *Philosophical Trans Royal Soc B: Biol Sci* 372:20160135. doi.org/10.1098/rstb.2016.0135
74. Urban J, Ingwers MW, McGuire MA, Teskey RO (2017) Increase in leaf temperature opens stomata and decouples net photosynthesis from stomatal conductance in *Pinus taeda* and *Populus deltoides* X *Nigra*. *J Exp Bot* 68:1757–1767. doi.org/10.1093/jxb/erx052
75. Wahid A, Gelani S, Ashraf M, Foolad MR (2007) Heat tolerance in plants: an overview. *Environ Exp Bot* 61:199–223. doi.org/10.1016/j.envexpbot.2007.05.011
76. Warren CR (2006) Why does photosynthesis decrease with needle age in *Pinus pinaster*? *Trees* 20:157–164. doi.org/10.1007/s00468-005-0021-7
77. Woodruff DR, Meinzer FC (2011) Water stress, shoot growth and storage of non-structural carbohydrates along a tree height gradient in a tall conifer. *Plant Cell Environ* 34:1920–1930.
doi.org/10.1111/j.1365-3040.2011.02388.x
78. Zhou S, Williams AP, Berg AM, Cook BI, Zhang Y, Hagemann S, Lorenz R, Seneviratne SI, Gentile P (2019) Land–atmosphere feedbacks exacerbate concurrent soil drought and atmospheric aridity. *Proceedings of the National Academy of Sciences* 116:18848–18853.
doi.org/10.1073/pnas.1904955116

Figures



Figure 1

(a) Panoramic view of the open-field experimental site and (b) three-year-old *Pinus densiflora* seedlings ($n = 28$) planted in a plot of 2.5 m^2 ($1 \text{ m} \times 1.5 \text{ m}$).

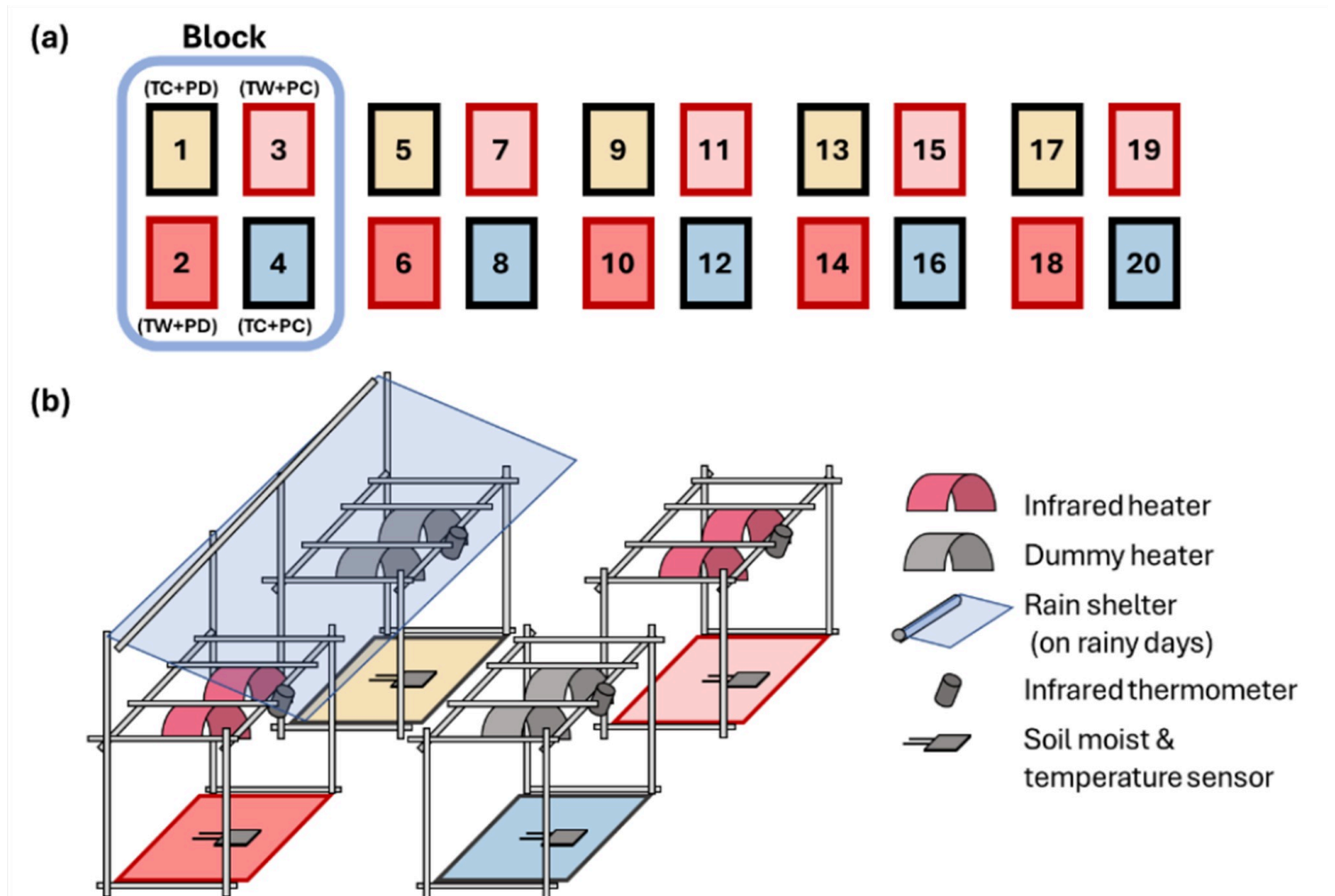


Figure 2

(a) Plot layout in the open-field experiment and (b) design of an automatic warming and drought system using infrared heating lamps for extreme warming and rain shelters for extreme drought. TC+PC: control (i.e., no warming and drought) treatment, TC+PD: drought only treatment, TW+PC: warming only treatment, and TW+PD: warming + drought treatment.

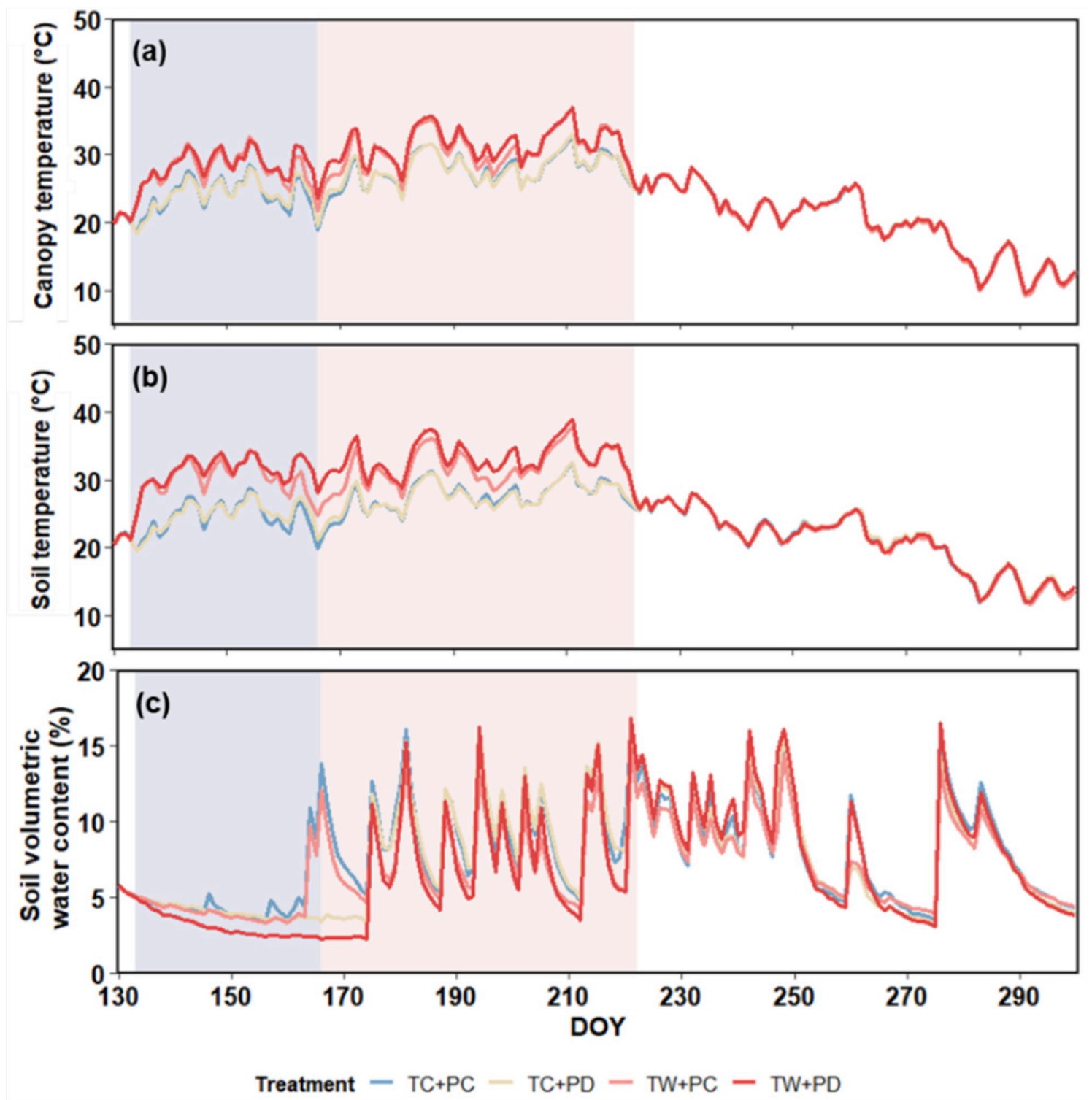


Figure 3

Daily average (a) canopy temperature (°C), (b) soil temperature (°C), and (c) soil volumetric water content (VWC, %) during the experimental period according to the extreme warming and drought treatments. The blue shadow indicates the temperature and precipitation manipulation period (Period 1; DOY:133-166), and the pink shadow indicates the temperature manipulation period (Period 2; DOY: 166-222). DOY 223 to 311 represents the post-manipulation period (Period 3).

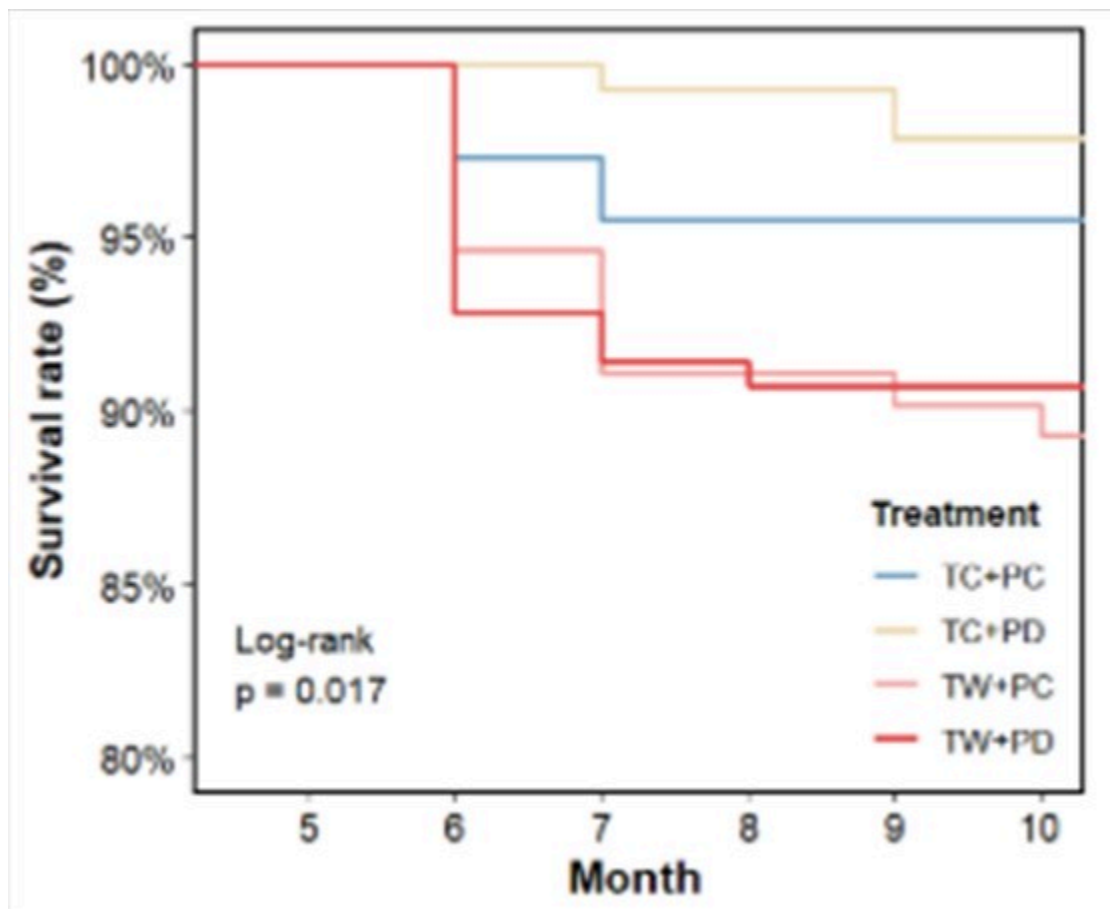


Figure 4

Kaplan–Meier survival curves of *Pinus densiflora* seedlings under extreme warming and drought treatments from May to October 2022. TC+PC: control (i.e., no warming and drought) treatment, TC+PD: drought only treatment, TW+PC: warming only treatment, and TW+PD: warming + drought treatment.

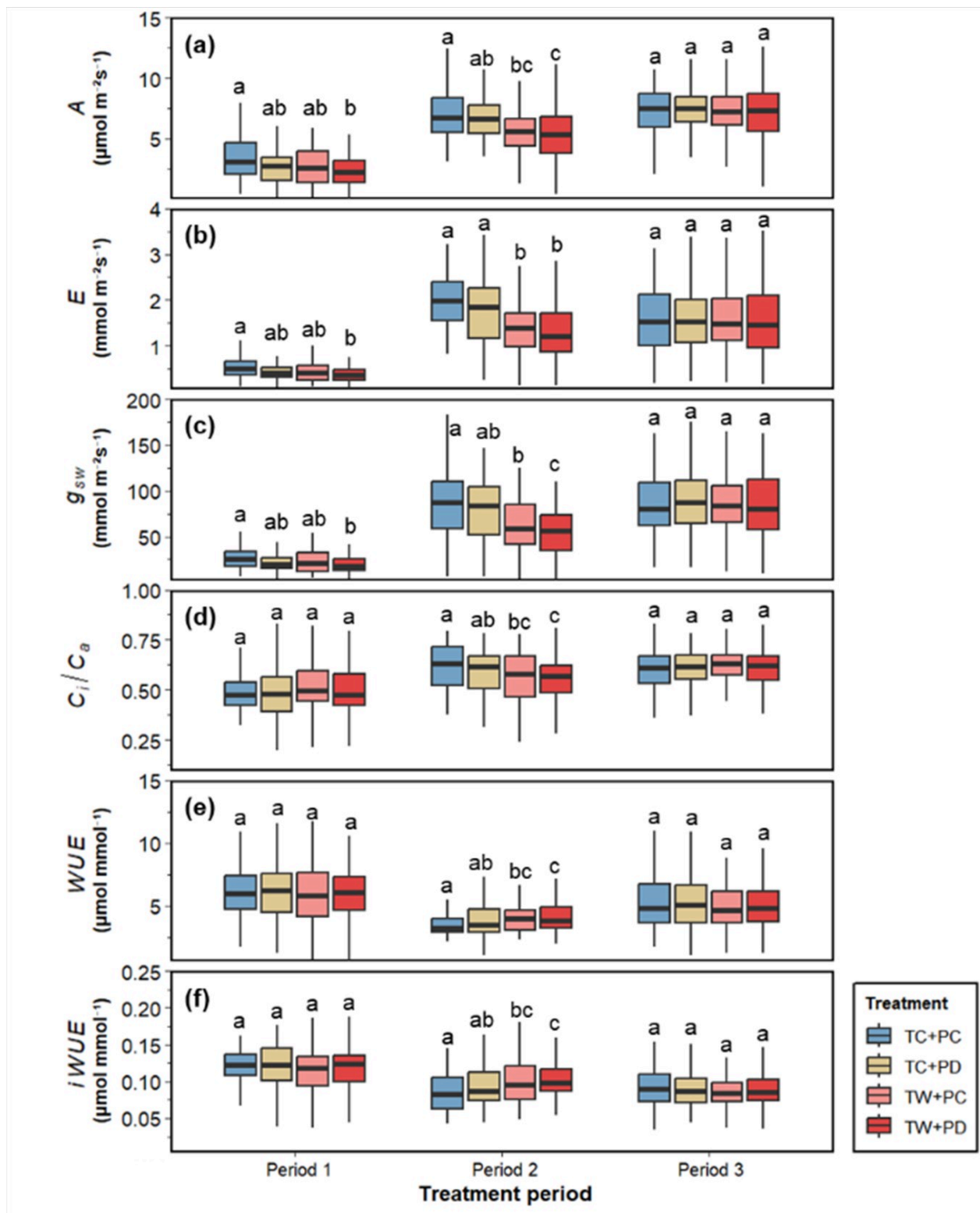


Figure 5

(a) Net photosynthesis rate (A), (b) transpiration rate (E), (c) stomatal conductance (g_{sw}), (d) intercellular to ambient CO_2 concentrations ratio (C_i/C_a), (e) instantaneous water use efficiency (WUE), and (f) intrinsic water use efficiency ($iWUE$) of *Pinus densiflora* seedlings according to the periods of treatment manipulation (Periods 1–3) under extreme warming and drought treatments. The bars topped with

different superscripts indicate significant differences between treatments according to the Tukey post-hoc test.

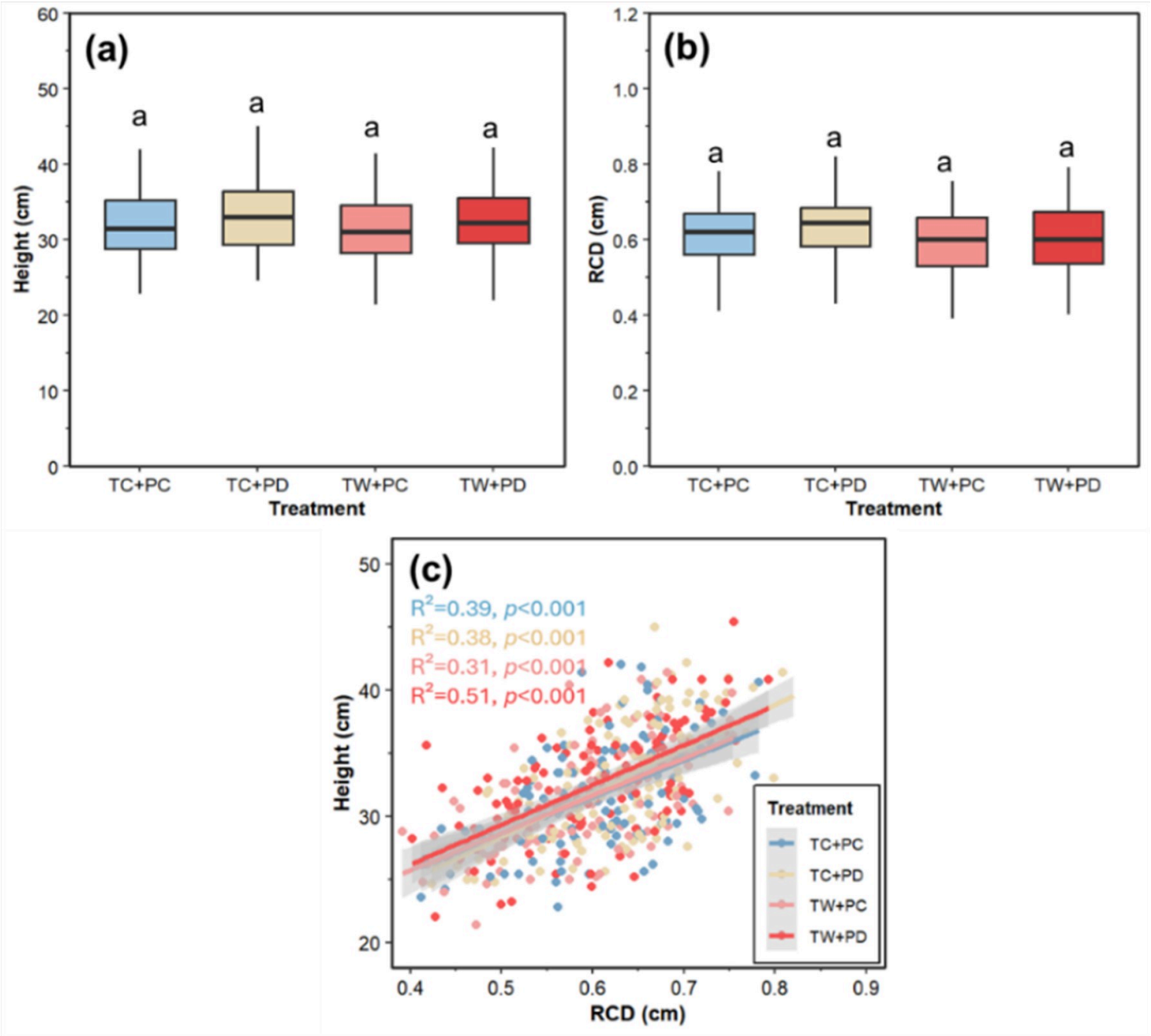


Figure 6

a) Height, (b) root collar diameter (RCD), and (c) relationship between height and RCD of *Pinus densiflora* seedlings under extreme warming and drought treatments. The bars topped with different superscripts indicate significant differences between treatments according to the Tukey post-hoc test.

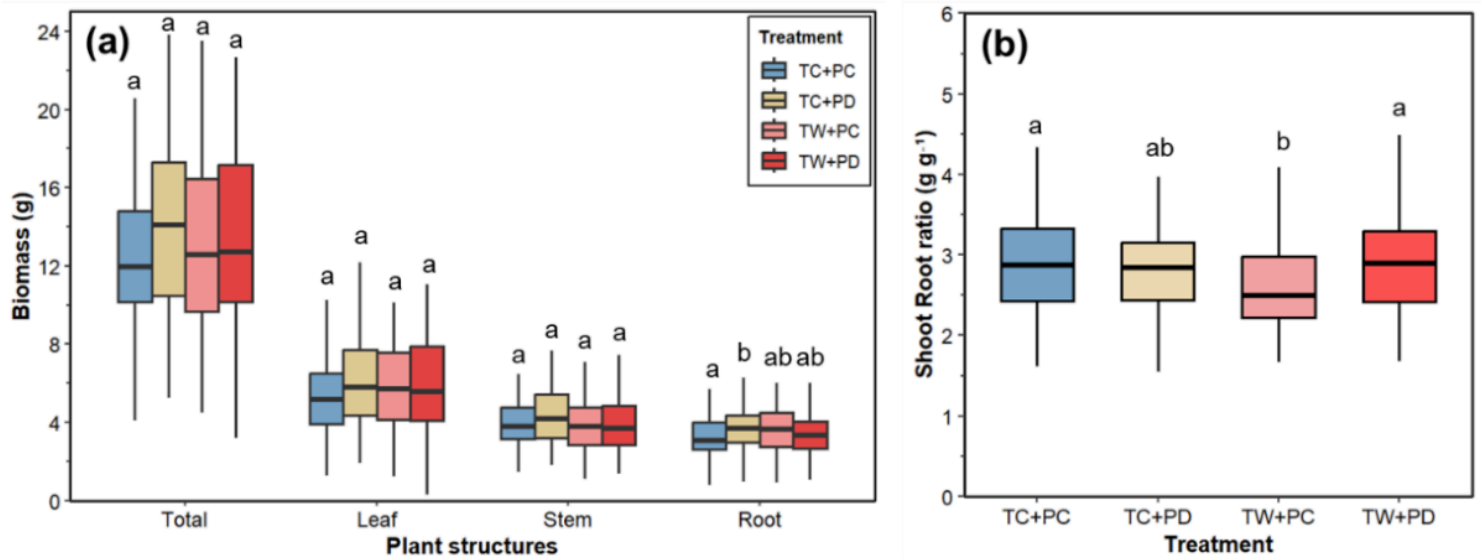


Figure 7

a) Biomass allocation among fractions and (b) shoot: root biomass ratio ($S:R$) of *P. densiflora* seedlings under extreme warming and drought treatments. For each biomass fractions, bars topped with different superscripts indicate significant differences between treatments according to the Tukey post-hoc test. Descriptions of the treatment acronyms and boxplots are provided in Figures 1 and 3, respectively.

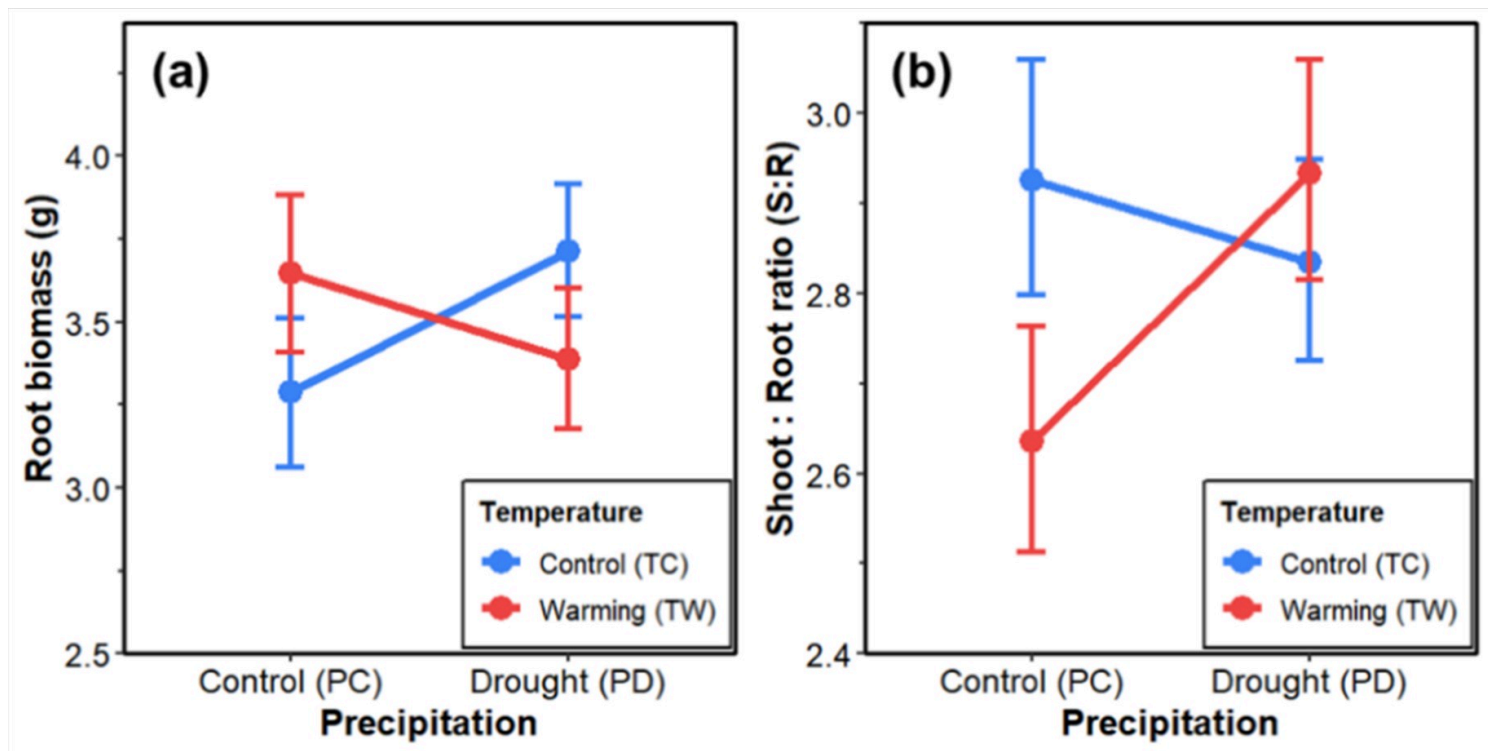


Figure 8

Interactive effects of extreme warming and drought on (a) root biomass and (b) shoot: root biomass ratio ($S:R$) of *Pinus densiflora* seedlings. Lines connect predicted means under temperature control (PC,

blue) and warming (PW, red) across extreme drought treatments (PC and PD). Non-parallel lines indicate significant warming and drought interaction ($p < 0.05$).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [SupplementaryTable.docx](#)