

Article

Effects of Spring Warming and Drought Events on the Autumn Growth of *Larix kaempferi* Seedlings

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Abstract: High temperatures and droughts following winter dormancy can negatively affect seedling growth and mortality. An open-field experiment was conducted to study the growth and mortality of *Larix kaempferi* seedlings in response to spring warming and drought treatments and to determine whether seedlings could regain their growth capability once the treatments were discontinued. In May 2020, 1-year-old seedlings were exposed to four treatments: control, warming-only, drought-only, and the combined warming and drought. Drought treatment reduced the seedling height and root collar diameter and increased the mortality rate. The combined warming and drought treatments had the highest mortality rates, followed by the drought, control, and warming treatments. However, after the cessation of the treatments, the combined warming and drought treatments increased seedling height, root collar diameter, and individual seedling biomass because the high mortality rate relaxed competition among seedlings. This suggests that the effects of low competition on the surviving seedlings may mitigate the negative effects of warming and drought on seedling growth. Our study demonstrates that despite the high mortality and decreased growth during the treatment period, seedlings subjected to combined high temperature and drought stress showed short-term high levels of growth compared to seedlings subjected to a single stress.

Keywords: climate change; drought; growth; *Larix kaempferi*; mortality



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1. Introduction

Human-induced warming reached approximately 1 °C above the pre-industrial global temperature levels in 2017, increasing at a rate of 0.2 °C per decade [1]. At the same time, climate change has generally accelerated the hydrological processes, resulting in more intense and frequent drought events [2]. The Intergovernmental Panel on Climate Change (IPCC) predicted that the increase in global temperature and drought events will gradually deteriorate, especially in terrestrial regions [3]. Those changes in climate will trigger a wide range of impacts on forest ecosystems, including direct impacts on trees such as increased mortality, decrease in growth rate, and reduced regeneration success [4–6].

As spring is the growing season, plants are more sensitive to environmental stresses compared to other seasons. Changes in spring temperature and precipitation substantially impact the structure and functioning of ecosystems by affecting plant phenology and growth [7,8]. Warmer springs may cause the positive or negative lagged effects on plants' productivity during the following summer and autumn [9]. Richardson et al. [10] who investigated relationships between surface-atmosphere CO₂ fluxes and interannual variation in a boreal-northern forest, showed that the earlier spring might accelerate N mineralization, and thus, photosynthetic activities could be increased as a result of higher foliar N concentrations over the entire growing season. In contrast, warmer springs could trigger a decrease in the productivity of plants in the subsequent seasons through the water

deficit [11]. In addition, drier springs could affect leaf life span, resulting in earlier autumn senescence [12,13]. The impact of spring drought on plants would be greater because spring droughts have increased their intensity due to climate change in recent years [14].

To understand the response of trees to environmental change, researchers have manipulated air temperature and precipitation in numerous field experiments [15–17]. Climate manipulation experiments can be useful tools to figure out the responses of trees to climate change since the manipulative experiments allow researchers to pinpoint the mechanisms between environmental factors and ecosystems [18]. Jo et al. [19] and Chang et al. [20] reported that the experimental +3 °C warming using an infrared heater might induce a decrease in photosynthetic activities of coniferous seedlings, potentially resulting in an increase in mortality rate. Using a mobile rainout shelter, Misson et al. [21] simulated drought in the Mediterranean forest and showed that spring drought can inhibit foliar and floral development of *Quercus ilex* by affecting the phenophase progression. In the experiment of Rizhsky et al. [22], *Arabidopsis* plants could open their stomata due to the extremely high leaf temperature under the combined warming and drought treatment.

Larix kaempferi is a major plantation species with fast-growing characteristics and accounts for 32% of the total plantation area in South Korea [14,23]. The production of *L. kaempferi* seedlings is steadily increasing as demand for timber has increased [14,23]. However, *L. kaempferi* is known for being highly vulnerable to climate change [24]. In the experiment of An et al. [25], the +3 °C warming treatment significantly limited leaf gas exchange of 2-year-old *L. kaempferi* seedlings. Kwon et al. [26] showed that the mortality rate of *L. kaempferi* increased under the increased temperature and decreased precipitation, and the seedling quality index was low in the increased precipitation treated group. In addition, Bhusal et al. [14] revealed that the maximum photosynthetic rate of *L. kaempferi* seedlings can be decreased by approximately 48% compared to that of the control under drought stresses. However, few studies have examined the effects of warming and drought on *L. kaempferi* in the spring season, and even fewer have examined the effects on *L. kaempferi* for an extended period after the cessation of the treatments. It is necessary to understand how excessively high temperatures and drought might influence *L. kaempferi* seedlings in the spring and how their response is altered after a period of warming and drought.

In this study, an open-field manipulation system was used to simulate the spring warming and drought of Seoul in the 2070s for *L. kaempferi* seedlings. Among all growing stages, the seedling stages are particularly susceptible to changes in environmental conditions due to the immature state of their roots and stems [27]. Regarding the long-term performance of tree species which is highly related to the seedling stage, it is important to determine the response of seedlings under the changing environments to understand the overall performance of trees [28]. The objectives of this study were to figure out the growth and mortality of *L. kaempferi* seedlings under the spring warming and drought treatment, and to determine whether the seedlings can recover from the heat and drought stresses during the subsequent summer and autumn.

2. Materials and Methods

2.1. Experimental Warming and Drought Treatments

The experimental site was located in an open-field nursery site at the Korea University Green Campus in Seoul, South Korea (37°35'36" N, 127°1'31" E). The area has a moderate climate, with annual mean precipitation of 1450.5 mm (61% of which occurs during June through August) and an annual mean temperature of 12.5 °C [29]. The soil texture was sandy loam. The acidity (pH) of the soil was 6.52, carbon content was 0.22%, and nitrogen content was 0.05%.

In March 2020, the experimental plots were established in March 2020. In April, seedlings had a rest period for a month to develop a root system and get accustomed to the soil. In May, 1-year-old *L. kaempferi* seedlings were exposed to two different temperature conditions (ambient temperature and a 4 °C increase in the second and fourth weeks of May) and two different precipitation conditions (ambient precipitation and precipitation

blocking in all four weeks in May). Five 1.0 m × 1.5 m plots were established for each of the four treatments (a total of twenty plots): control, warming-only, drought-only, and the combined warming and drought. A total of 80 1-year-old *L. kaempferi* seedlings were planted in each plot (Figure 1). The seedlings were chosen based on the quality standard of forest seeds by the National Forest Seed and Variety Center and were genetically homogeneous.

Environmental factors were manipulated to simulate the spring environment of Seoul in the 2070s. Under the Representative Concentration Pathway (RCP) 8.5 scenario which predicted climate change until 2100 in Seoul, Korea, the average spring temperature is predicted to increase from 12.6 °C (2011–2020) to 16.7 °C (2071–2080), and the maximum consecutive dry days is projected to increase from 29.3 days (2011–2020) to 29.8 days (2071–2080) [29]. Accordingly, the warming treatment was designed to increase the air temperature by 4 °C and the drought treatment was designed to simulate 30 days of precipitation reduction [1,29].

Infrared heaters hanging 60 cm above the average seedling height were established to increase the temperature in the warming plots. As infrared heaters cast shadows over plots, two dummies with the same shape and size as the infrared heater were also established in the control and the warming-only plots. An automatic rainout shelter was installed 1.6 m above the ground to completely block rain in the drought plots. The rainout shelters were coiled onto a beam when there is no rain and automatically opened when an electronic controller detects rain. Infrared thermometers (SI-111; Campbell Scientific Inc., Logan, UT, USA) and soil temperature moisture sensors (CS655; Campbell Scientific Inc., Logan, UT, USA) were placed in each plot to measure air temperature, soil temperature, and soil moisture content. These environmental data were collected every half-hour by using a data logger (CR1000X; Campbell Scientific Inc., Logan, UT, USA).

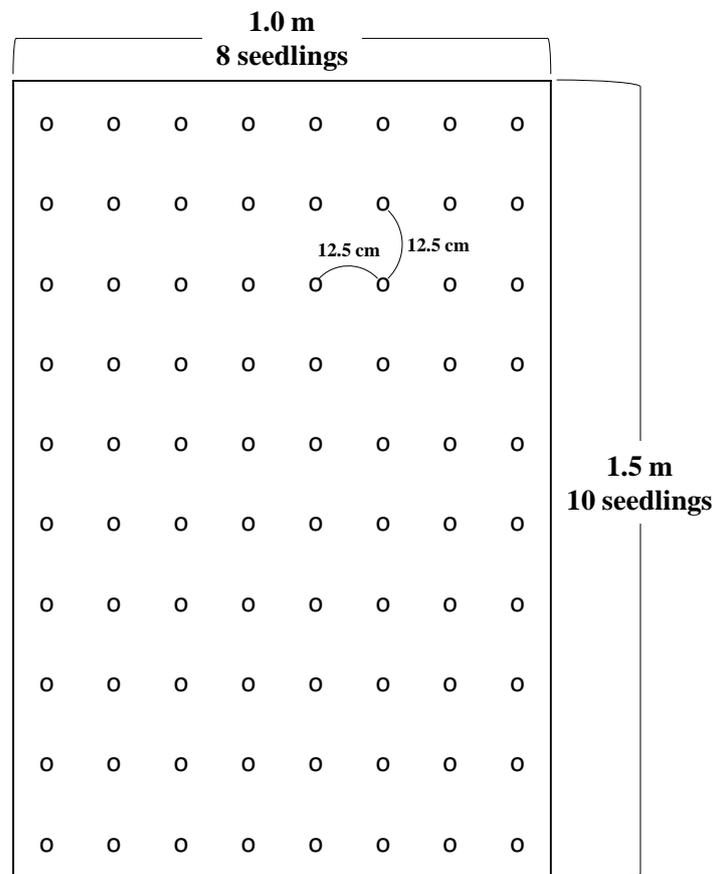


Figure 1. Seedling arrangement and spacing per plot.

2.2. Seedling Growth and Mortality Rate

We measured all the seedlings' height and root collar diameter on 30 April (right before the treatment started), 1 June (right after the treatment ceased), and 30 October (when the growing season ended). Seedling height was measured using a folding ruler. Root collar diameter was measured 1 cm above the ground using a digital caliper. At the end of the growing season, five randomly chosen seedlings from each plot were harvested, and their biomasses were measured. Manual excavation was used to retrieve as many roots as possible from the seedlings. Seedlings were collected; partitioned into stems, leaves, and roots; dried at 65 °C, and weighed to the nearest 0.01 g. The mortality rate was quantified at the end of the growing season (1).

$$\text{Mortality rate (\%)} = \frac{\text{Number of dead seedlings per plot}}{80 (\text{Total number of seedlings per plot})} \times 100 \quad (1)$$

2.3. Data Analysis

The effects of artificial warming and drought and their interaction on air temperature, soil temperature, soil moisture content, seedling height, root collar diameter, biomass, and mortality were analyzed using two-way ANOVA. Tukey's test was used to determine whether individual treatments were significantly different at a 0.05 probability level. Additionally, linear regression was used to analyze relationships between mortality rate and biomass of leaves, stems, and roots, and the total biomass. SAS version 9.4 was used for all statistical analyses (SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Experimental Warming and Drought Treatments

During the second and fourth weeks in May when infrared heaters were activated, both warming and drought treatments increased air temperature (Figure 2a). Air temperature in the control, warming-only, drought-only, and combined warming and drought plots were 19.1, 23.5, 20.1, and 24.3 °C in the second week and 19.8, 23.1, 20.8, and 24.0 °C in the fourth week, respectively. On average, the increase in air temperature by the warming and drought treatments were 4.0 and 1.0 °C, respectively. Additionally, the warming and drought treatments elevated soil temperature significantly during the warming treatment period (Figure 2b). Soil temperatures in the control, warming-only, drought-only, and combined warming and drought plots were 20.4, 24.9, 22.0, and 26.5 °C in the second week and 20.0, 25.5, 22.1, and 27.2 °C in the fourth week, respectively. On average, the increase in soil temperature by the warming and drought treatments were 5.0 and 1.9 °C, respectively. Although the infrared heaters were not activated in the third week, soil temperature in the warming-only plot was higher than that in the control plot by 0.5 °C.

The mean soil moisture content of the control plot in the first, second, third, and fourth weeks in May were 2.4, 4.1, 7.5, and 5.4%, respectively (Figure 2c). In the first week, the drought treatment significantly decreased soil moisture content by 0.04%. In the second week, the warming and drought treatments decreased soil moisture content by 2.0 and 0.4%, respectively. The warming and drought treatments decreased soil moisture content, but the warming treatment decreased the decreasing impact of the drought treatment on soil moisture content in the third and fourth weeks. In the third week, the drought treatment without warming decreased soil moisture content by 4.5%, but the drought treatment with warming decreased soil moisture content by only 4.3%. Similarly, in the fourth week, the drought treatment without warming decreased soil moisture content by 3.5%, but the drought treatment with warming decreased soil moisture content by only 3.0% in the third week.

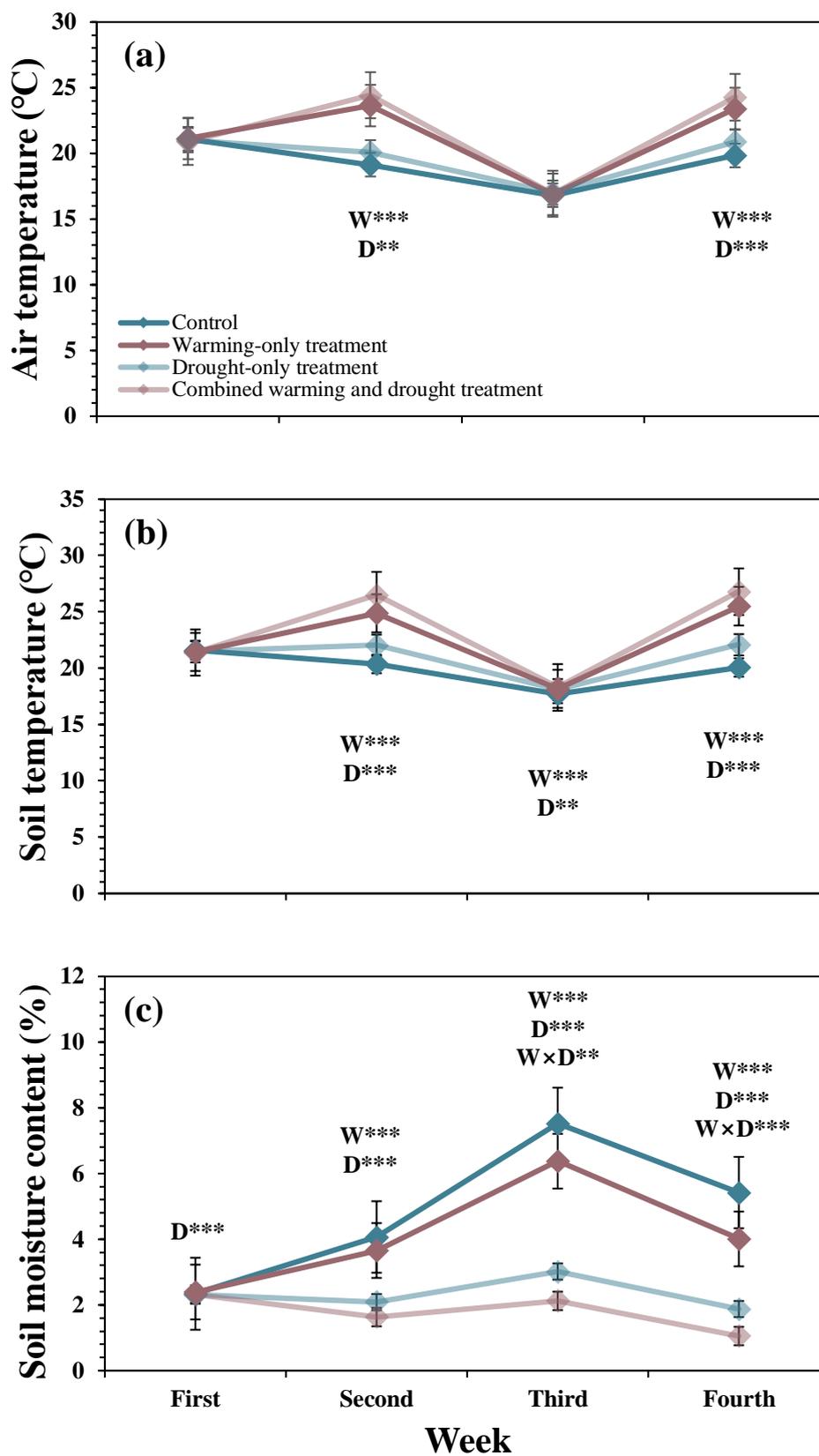


Figure 2. Mean weekly changes in air temperature (a), soil temperature (b), and soil moisture content (c) in May 2020. Error bars are the standard errors of the means, and asterisks (*) indicate significant differences between the warming and drought treatments (** $p < 0.01$; *** $p < 0.001$). W: warming effect; D: drought effect; W × D: interaction effect of warming and drought.

3.2. Seedling Height and Root Collar Diameter Response

In the treatment period (i.e., in May), the height increment was largest in the control plots by $2.2 \text{ cm month}^{-1}$ and lowest in the combined warming and drought plots by $3.0 \text{ cm month}^{-1}$ (Figure 3a). In this period, the drought treatment significantly decreased height increment; however, there was no significant effect of warming on height increment, and there was a significant interaction effect between warming and drought. The drought treatment without warming decreased height increment by $0.91 \text{ cm month}^{-1}$, but the drought treatment with warming decreased height increment only by $0.83 \text{ cm month}^{-1}$. However, until the end of the growing season after the treatment period (i.e., during June through October), there was no significant difference in height increments in the control and the combined warming and drought plots. Moreover, there were no significant impacts of warming and drought treatments on height increment, yet there was a significant interaction effect between these two treatments.

In the treatment period, root collar diameter increment was largest in the control plots by $0.6 \text{ cm month}^{-1}$ and lowest in the combined warming and drought plots by $0.2 \text{ cm month}^{-1}$ (Figure 3b). In this period, the drought treatment significantly decreased root collar diameter increment. However, until the end of the growing season after the treatment period (i.e., during June through October), the root collar diameter increment in the combined warming and drought plots was larger than that in the control plots. Moreover, the drought treatment significantly affected root collar diameter increment, while there was no significant effect of the warming treatment. Additionally, there was a significant interaction effect between warming and drought treatment; the drought treatment without warming increased height increment by $0.02 \text{ cm month}^{-1}$, but the drought treatment with warming decreased height increment only by $0.10 \text{ cm month}^{-1}$.

3.3. Biomass and Mortality Rate

The average individual biomass of leaf, shoot, root, and the total in the control plots were 4.4, 5.6, 3.0, and 12.9 g, respectively (Figure 4). Leaf, shoot, and total biomass were greater in the combined warming and drought treatment than in the warming-only and drought-only plots. Meanwhile, there were no significant effects of warming and drought on the leaf, shoot, and total biomass, but there was a significant interaction effect between warming and drought treatments. However, there was no significant difference in root biomass among treatments nor significant effects of warming and drought treatments on root biomass.

The average mortality rate at the end of the growing season in the control, warming-only, drought-only, and combined warming and drought plots were 3.8, 1.8, 5.3, and 8.5, respectively (Figure 5). In particular, the drought treatment significantly increased the mortality rate, and the mortality rate in the combined warming and drought plots was significantly higher than in the other plots.

There was a significant linear relationship ($p = 0.04$) between the mortality rate at the end of the growing season and the average individual biomass of leaf (Figure 6a). The leaf biomass increased by 1.3 g per 10% increase in mortality rate. Additionally, there was a quasi-significant linear relationship ($p = 0.07$) between the mortality rate and the average individual total biomass, showing a 2.6 g increase in total biomass per 10% increase in the mortality rate (Figure 6d). However, there were no significant linear relationships between the mortality rate and the average individual biomass of shoot and roots (Figure 6c,d).

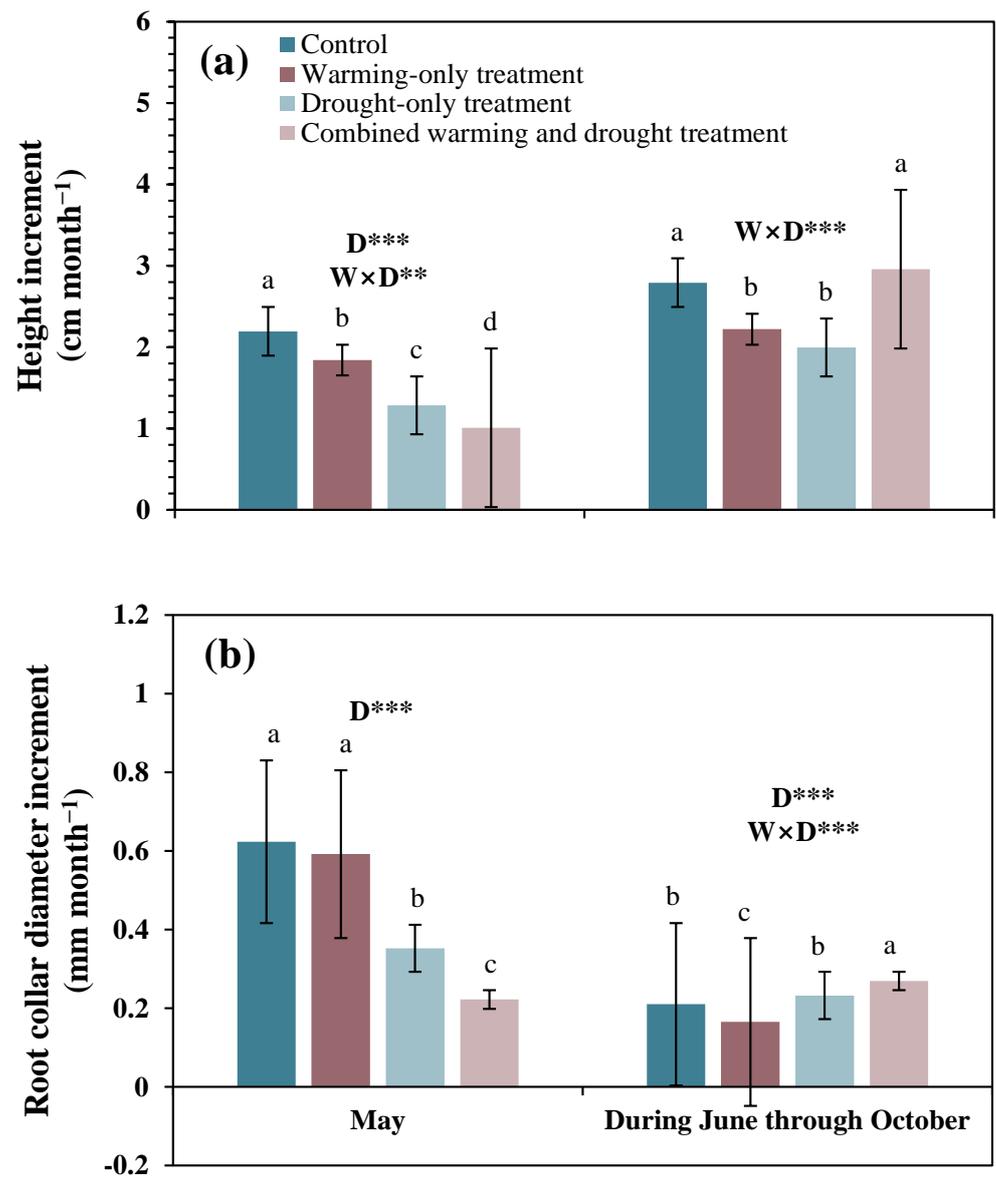


Figure 3. Height increment (a) and root collar diameter increment (b) of *Larix kaempferi* seedlings in 2020. Bars with different letters are significantly different among treatments at $p < 0.05$. Error bars are the standard errors of the means, and asterisks (*) indicate significant differences between the warming and drought treatments (** $p < 0.01$; *** $p < 0.001$). W: warming effect; D: drought effect; W × D: interaction effect of warming and drought.

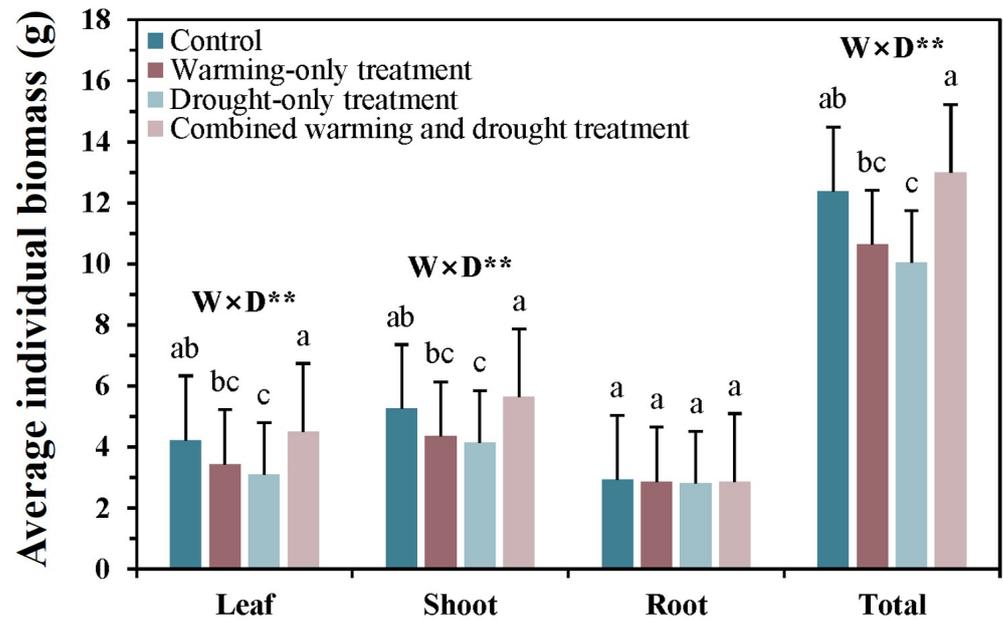


Figure 4. Average individual biomass of *Larix kaempferi* seedlings as influenced by warming and drought treatments in November 2020. Bars with different letters are significantly different among treatments at $p < 0.05$. Error bars are the standard errors of the means, and asterisks (*) indicate significant differences between the warming and drought treatments (** $p < 0.01$). W: warming effect; D: drought effect; W × D: interaction effect of warming and drought.

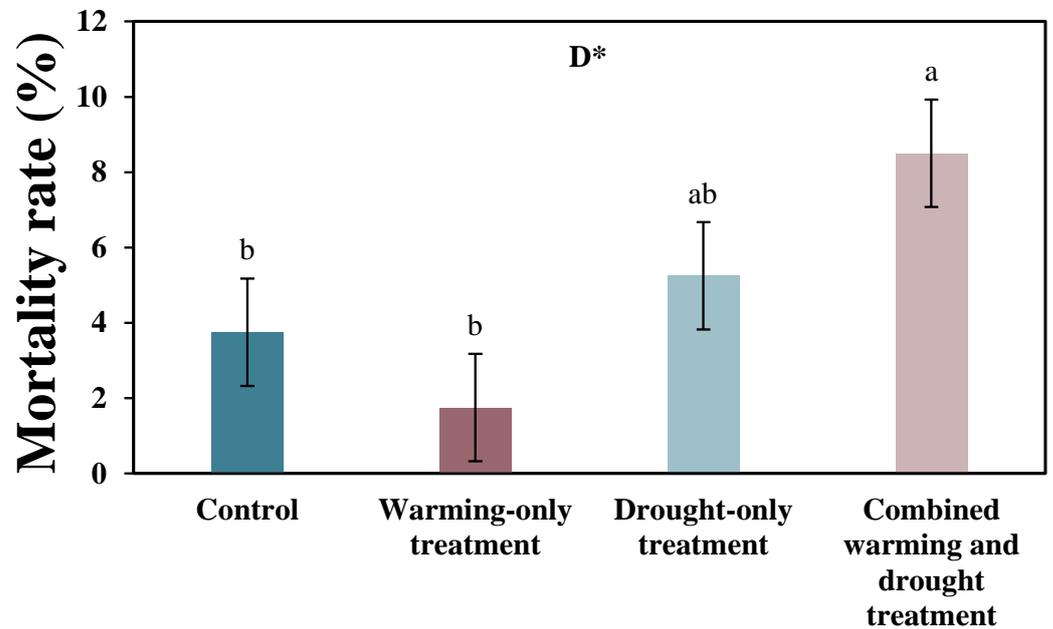


Figure 5. Mortality of *Larix kaempferi* seedlings in 2020. Bars with different letters are significantly different among treatments at $p < 0.05$. Error bars represent standard errors of the mean. The asterisk (*) indicates a significant difference in the drought treatment (* $p < 0.05$). D: drought effect.

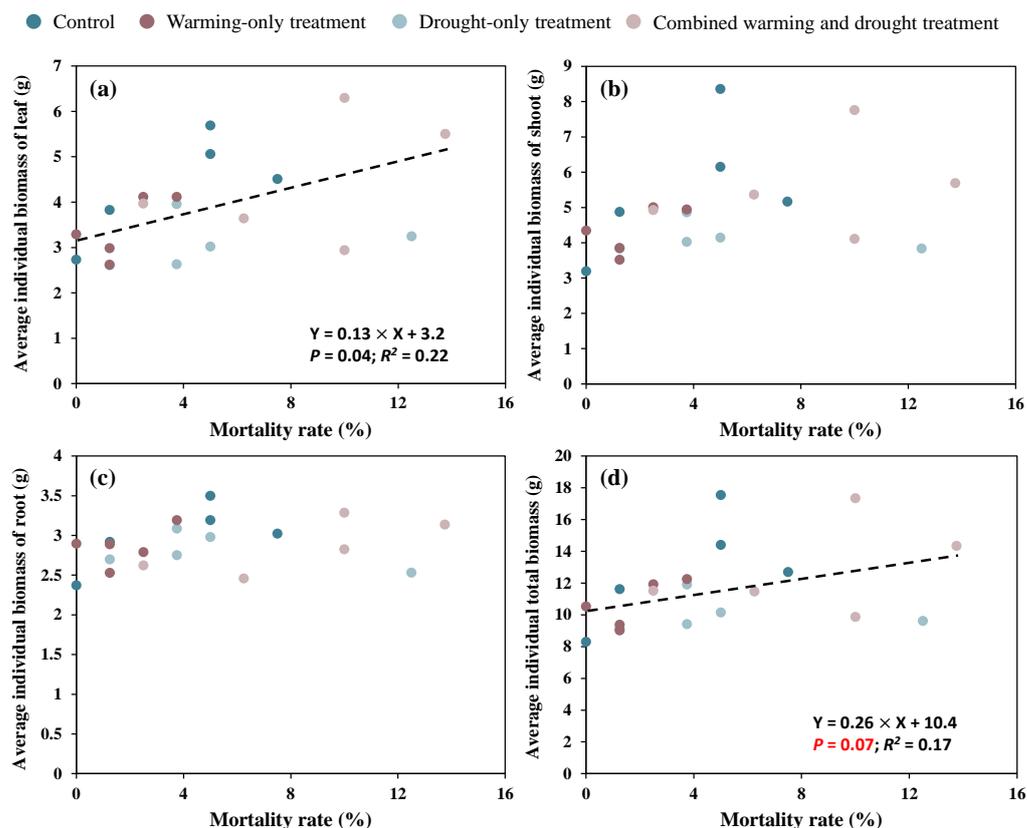


Figure 6. Relationships between the mortality rate at the end of the growing season and the average individual biomass of leaf (a), shoot (b), root (c), and the total biomass (d). Black dashed lines indicate linear relationships between two variables.

4. Discussion

The increase in air temperature by 4.0 °C under the warming treatment and the decrease in soil moisture content under the drought treatment showed that our climate manipulation system was operating properly (Figure 2). Meanwhile, our findings showed that the drought treatment increased the mortality rate (Figure 5). These results are consistent with those of prior research, which showed that the 1982–1983 El Niño-related drought was associated with increased seedling mortality rates [30]. In general, soil moisture conditions are significant for the survival of seedlings in the early stage. In the case of anisohydric plants, stomatal closure does not occur even during the drying period. Therefore, the leaf moisture potential remains high [26]. Our findings suggested that *L. kaempferi* exhibits anisohydric characteristics [26]. Under the reduced moisture conditions, the survival rate was lowered by continuing gas exchange without closing the stomata until death due to water loss.

However, the warming treatment did not significantly affect the mortality rate by itself (Figure 5). Similar effects of increased temperature on the mortality rate of seedlings have been previously reported; the seedling survival rate of *Pinus densiflora* showed no significant difference when experimental warming increased by 3 °C [26,31]. The increased air temperature in this study (i.e., 4 °C) may have been insufficient to induce substantial changes in the mortality rate. In addition, the drought treatment was carried out for four consecutive weeks, whereas the warming treatment had a rest period in the middle (i.e., the third week in May).

Our results are in line with previous studies where warming and drought treatments constrain seedling height and root collar diameter increments but only immediately after treatment. In our experiment, seedling height and root collar diameter increments decreased under drought treatments, consistent with previous findings with *Abies fabri* [32]. This

suggests that our drought treatments induced heat and water stress in *L. kaempferi* seedlings. However, the analyses of seedling height, root collar diameter, and biomass five months after treatment revealed that seedlings exposed to the combined treatment had the highest mortality rates but showed the highest growth. Geange et al. [33] reported similar results in *Aciphylla glacialis*. Environmental stress significantly increased seedling mortality, but the surviving seedlings grew better than their counterparts.

The positive effects of environmental stress on plant growth have been poorly discussed in the literature, and the mechanisms remain unknown [34]. Moreover, few studies have shown that high temperature and drought stress can trigger a series of physio-biochemical compensations in plants. The higher growth in the combined warming–drought treatment might be due to overcompensation [35] for the disappearance of the stressful treatments, the low competition effect [36] of the surviving seedlings, and the development of adaptive mechanisms by slowly increasing stress. Numerous variables, such as genotype, nutritional status, light, competition with other plants, plant phenology, plant size, severity and length of drought, and rehydration duration, impact the physiological and morphological characteristics of re-watered plants [37].

Overcompensation is typically associated with a hormetic effect, which occurs when the homeostasis of an organism is disturbed [38–41]. If cells are exposed to stresses that disrupt homeostasis, the unfolded protein response, endoplasmic reticulum-associated degradation, and the heat shock response will all become active to aid recovery [42]. It has been shown that activating the heat shock response results in increased amounts of heat shock proteins, which alleviate a load of aberrant proteins by enabling them to refold their original shape [43]. Cells also demonstrate higher concentrations of components from the ubiquitin-proteasome system after being exposed to stress, and as a result, they have a greater ability to destroy proteins that cannot be refolded as a result [44]. The modulation of heat shock protein levels and overexpression of ubiquitin-proteasome system components may be stated to be a reliable molecular basis for the positive effects of hormesis [42]. Wei et al. [45] found that the net photosynthetic rate, stomatal conductance, soluble protein, malondialdehyde, and chlorophyll content increased at 6–9 days after high-temperature stress, which was a significant driving factor for the compensatory growth of *Brassica rapa*. Zhou et al. [46] discovered that after 6 days of drought stress and rehydration, proline, soluble protein, superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) activity significantly increased. High levels of SOD and CAT may successfully eliminate reactive oxygen species and APX enzyme activity could mitigate membrane damage and lipid peroxidation [47].

Another possibility is that seedlings in the combined warming–drought treatment experienced decreased intraspecific competition as the mortality rate increased. Several researchers have observed that intraspecific competition reduces plant biomass [48,49]. An increased plant density may result in an asymmetrical frequency distribution of plants, resulting in size variations among individual plants [50]. For instance, if there is competition for water, individuals with more extensive roots may reduce the water available to ones with smaller roots, thereby suppressing their development. In addition, in a symmetrical competitive response, the biomass production of each individual declines uniformly [49]. Horner et al. [51] discovered that high-density stands were dominated by thin trees. In contrast, low-density stands generated distributions with a broad range of stem sizes and a high mean and maximum stem diameter.

Slowly increasing stresses may produce physiological adaptations that protect plants against the growth inhibition and damage that result from suddenly applied environmental stresses [52]. The stress imposed in our experiment could correspond to a slowly increasing stress, so a mechanism protecting the plants may have been at work. The exposure of plants to sub-lethal high temperatures can enhance their thermotolerance [53]. Potential modes of the reaction include the formation of heat-shock proteins, isoprene, and antioxidants to safeguard the photosynthetic apparatus and cellular metabolism [52]. Seedlings previously subjected to water stress often experience less inhibition of develop-

ment and other processes upon transplantation than seedlings not previously subjected to water stress [54]. Typically, controlled wetting and drying cycles promote early bud break, dormancy, and drought resistance [55]. In many species, improved drought tolerance is connected with osmotic adjustment, including the buildup of osmotically active chemicals after such cycles [52].

However, the drought-only treated seedlings, which had a high mortality rate due to drought stress, did not show as much recovery as the combined warming–drought treatment. This might be due to the combined stress inducing different, and sometimes antagonistic, signaling pathways [56]. In particular, plants growing in the field are subjected to diverse co-occurring abiotic stimuli that most likely cannot be extrapolated from the sum of individual stresses that affect plant metabolism in unique ways [57]. Similar findings have been obtained for *Pinus sylvestris* [58] under heat and drought conditions and under herbivory and competitive conditions [59]. These findings demonstrate superior stress resistance and resilience of *L. kaempferi* even when the mortality rate increases.

5. Conclusions

In our study, warming and drought treatments increased the mortality rate and decreased growth during the treatment period. However, after the cessation of the treatment, seedlings in the combined warming and drought plots showed higher individual biomass growth compared to seedlings that experienced either warming or drought treatment. We suggest that this is because the higher mortality rate under the combined warming and drought plots might result in relaxation in seedling competition for resources, such as water, light, and nutrients, which can lead to an increase in individual biomass growth. However, these mechanisms do not necessarily lead to a positive effect during early spring warming and drought stress in *L. kaempferi* seedlings. Extreme and persistent stresses are likely to result in a reduction in growth and high mortality rates. Therefore, even if 1-year-old *L. kaempferi* seedlings experience spring warming and drought events at a similar level to this study in the future, it is expected that the reduction in growth will sufficiently recover when they are exposed to the average temperature and precipitation in summer and autumn. To accurately predict stress response dynamics under climate change, further studies should be conducted on various stress levels, molecular-based protection mechanisms, such as the antioxidant systems, and distance independent competition indices. In addition, it is necessary to collect information on lateral spread roots or foliage and whether the crowns were in contact to understand the response to competition better.

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