


## ORIGINAL ARTICLE

# Asymmetric Warming of Day and Night Benefits the Early Growth of *Acer mono* Seedlings More Than Symmetric Warming

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## ABSTRACT

Asymmetric warming refers to the difference between the increase in daytime maximum temperature and the increase in nighttime minimum temperature and has been documented in temperate regions. However, its impacts on seedling growth have been largely ignored. In this study, seedlings of a widely distributed tree species, *Acer mono* Maxim., were exposed to both symmetric warming (SW) and asymmetric warming scenarios (day warming [DW], night warming [NW] and diurnal asymmetric warming [DAW]). Compared to control, all warming scenarios were found to enhance belowground biomass. DW promoted the seedling growth, while NW reduced the stem biomass. DAW did not impact the total biomass relative to the control. Compared to SW, DAW advanced phenology, increased indole-3-acetic acid content and chlorophyll content, which enhanced total biomass and stored more NSC in the root. Future DAW would be not beneficial to the growth of *A. mono* seedlings by comparing with the control. This research encourages further exploration of tree growth experiments under asymmetric warming conditions, as most studies tend to underestimate the warming effects on plant growth by focusing on SW. Incorporating the responses of seedling physiology and growth to non-uniform diurnal warming into earth system models is crucial for more accurately predicting carbon and energy balances in a warmer world.

## 1 | Introduction

The surface air temperature over land during 2011–2020 has increased by 1.1°C compared to pre-industrial levels (1850–1900),

and it is predicted to further rise by around 4°C by the end of this century (IPCC 2023). Global warming has dramatically inhibited plant growth, which increases tree mortality and alters species' composition and biodiversity in temperate forests (Tao et al. 2022;

Thunell et al. 2023). However, warming is not diurnally and seasonally uniform, with notable asymmetric warming recorded not only at high latitudes but also in temperate regions (Piao et al. 2010). The temperate zone is particularly sensitive to global warming (IPCC 2023). Temperate forests play a pivotal role in the global carbon cycle, acting as a net carbon sink (accounting for 68% of the global forest net carbon sink) over the last two decades (2001–2019) (Partis et al. 2018; Pan et al. 2011). Photosynthesis, which occurs primarily during the daytime, is highly sensitive to the maximum daily temperature, while respiration persists throughout the day and is thus influenced by both the maximum and minimum daily temperatures (Peng et al. 2013). Warming has the potential to affect photosynthesis and respiration differently, thereby altering the balance of plants' net carbon exchange. Asymmetric warming could significantly alter the carbon dynamics of plants, particularly seedlings, due to their higher sensitivity to changing environmental conditions. However, seedlings' response to warming differ from those of adult plants, and previous studies have predominantly concentrated on the effects of daily mean temperature on seedlings, neglecting the asymmetric warming between day and night (Peng et al. 2013; Wang et al. 2021; Shi et al. 2023). This oversight will lead to inaccurate assessments of carbon sink and prediction in models and incompletely depict the genuine growth capabilities of tree species (Cox et al. 2020; Mu et al. 2021).

Elevated daily temperatures have been observed to enhance net photosynthetic rates, attributed to increased enzyme activity and chlorophyll content (Doughty and Goulden 2008; Vlam et al. 2013; Moore et al. 2021; Crous et al. 2022). This, in turn, promotes the production of auxin and gibberellins, thereby accelerating the growth rate. Ren et al. (2017) found that warming reduced indole-3-acetic acid (IAA) and increased abscisic acid (ABA), which regulates stomatal closure and ion channels, resulting in no impact on the growth of *Pinus yunnanensis*. Higher night temperature stimulates respiration, which hinders tree growth due to accelerated carbohydrate consumption (Clark et al. 2003; Phillips et al. 2011; Prasad and Djanaguiraman 2011). In previous studies, the elevated carbon loss caused by higher respiration under nighttime warming reduces tree growth (Clark et al. 2003; Liao et al. 2020) and the carbon sink of forests (Anderegg et al. 2015). Additionally, night warming (NW) resulted in higher antioxidant activities (i.e., superoxide dismutase [SOD], catalase [CAT]) of leaves due to higher malondialdehyde (MDA) content, implying that leaves are subjected to a stressed environment (Fan et al. 2017). Conversely, some studies suggested that NW might indirectly facilitate tree growth by stimulating compensatory photosynthesis the following day (Wan et al. 2009) or by reducing frost risk in early spring (Zhang et al. 2019). Moreover, a simplistic, carbon-centric perspective would overlook the reality that respiration serves as a productive process that fuels cellular activity (Slot and Winter 2018). Therefore, the response of seedlings' growth to asymmetric warming between day and night for trees is highly variable.

Empirical observations suggest minimum night temperatures are increasing more rapidly than maximum day temperatures, leading to a decline in the diurnal temperature range across various regions (Vose et al. 2005; Davy et al. 2017). The advancement of spring phenology could extend the growing

season, ultimately enhancing the total biomass of plants (Yan et al. 2020; Zohner and Renner 2019). Plants may lose more chilling at night compared to the forcing they gain during the day, resulting in an imbalance in forcing and chilling accumulations that could potentially alter phenology. As photosynthesis occurs only during the day and respiration occurs day and night, alterations in the diurnal temperature range (a reduction in diurnal temperature range) may disrupt the balance between photosynthesis and respiration. Reduced diurnal temperature range (i.e., asymmetric warming) may enhance night-time respiratory costs to a greater extent than it promotes photosynthesis. This imbalance can lead to a decreased accumulation of organic matter and non-structural carbohydrates in plants (Phillips et al. 2011; Prasad and Djanaguiraman 2011). Moreover, boosted respiration could reduce ABA content and carbohydrate concentration (Loka and Oosterhuis 2010; Antonietta et al. 2023; Wan et al. 2023). However, for temperate forests, little is known about the real effects of asymmetric warming between day and night on seedling growth, which could potentially impact the accuracy of evaluating carbon sequestration. Therefore, separately investigating the diverse responses of seedling growth and photosynthetic traits to day warming (DW) and NW is the key to understanding how seedlings' growth varies under asymmetric warming and symmetric warming (SW).

In the present study, we performed a non-uniform diurnal warming experiment using incubators to assess the growth, physiological traits and phenology responses of *Acer mono* Maxim., a maple species, to both asymmetric and symmetric warming. *A. mono* is a popular broad-leaved species extensively distributed in China, Japan, North Korea and Mongolia (Yu et al. 2014). It is also an important species for artificial afforestation, valued for its beautiful autumn foliage and its hard, stable, high-density wood used in furniture making (Kim et al. 2023). The main objectives were to determine (1) how DW and NW influence the growth of *A. mono* seedlings, and (2) how the difference between symmetric and diurnal asymmetric warming (DAW) impacts seedling growth. Specifically, we tested the hypotheses: (i) DW promotes seedling growth due to advanced phenology, enhanced photosynthesis (i.e., increased chlorophyll content) and IAA content; (ii) NW stimulates the growth of seedlings of *A. mono* due to compensatory photosynthesis and advanced phenology; and (iii) DAW promotes growth of seedlings of *A. mono* by advancing the phenological events and enhancing photosynthesis relative to SW.

## 2 | Materials and Methods

### 2.1 | Experimental Site and Plant Materials

In September 2020, the seeds of *A. mono* were collected from at least 15 mature mother trees at the Qingyuan Forest CERN (China Ecosystem Research Network) (41°55'27" N and 124°58'52" E). Only plump and intact seeds were kept for an experiment. These seeds underwent a 15-min soaking in a 0.1% sodium hypochlorite solution for disinfection, followed by thorough rinsing with clean water at least five times to eliminate any residue. After natural drying, the seeds were stored in a refrigerator

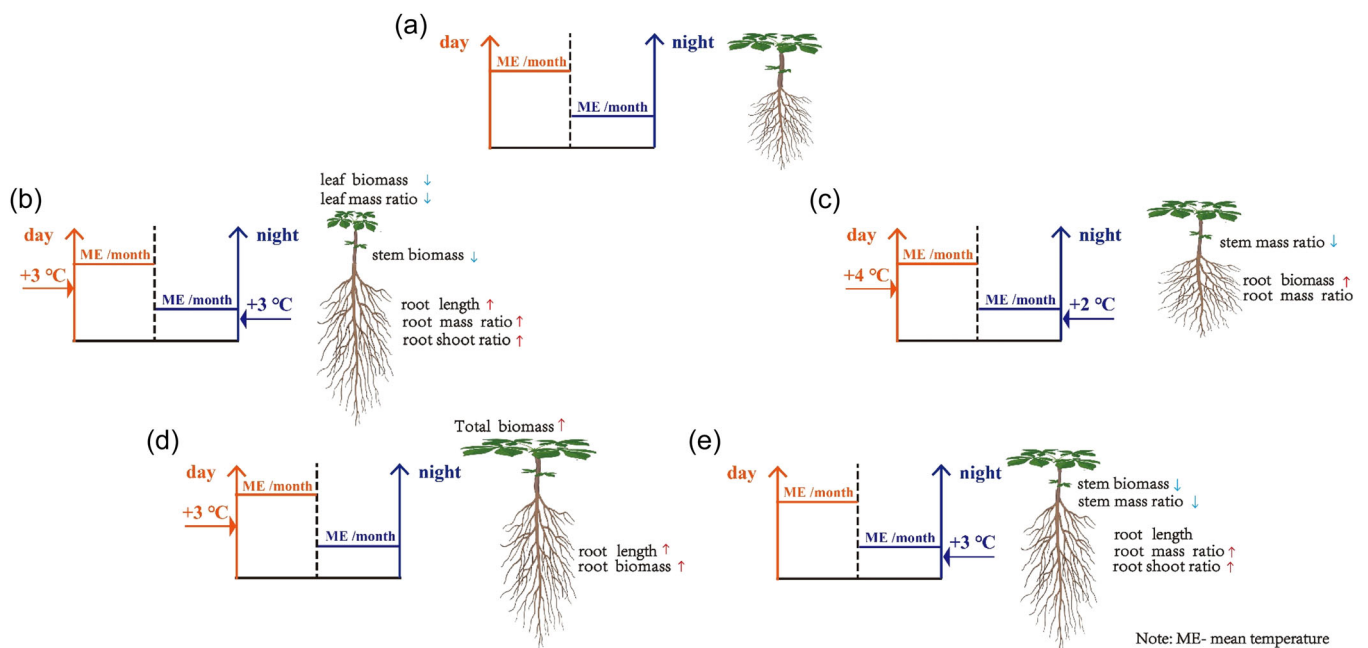
at  $-20^{\circ}\text{C}$ . In January 2021, seeds were subjected to sand stratification at  $4^{\circ}\text{C}$ , with 10 h of daily light ( $12.5\ \mu\text{mol m}^{-2}\text{s}^{-1}$ , the average under-canopy light intensity at the Qingyuan Forest CERN) and 14 h of darkness. The seeds were gently turned every 5 days and kept consistently moist. When 30%–40% of seeds germinated, they were sown in breeding trays, approximately 1 cm below the soil surface, with three seeds per tray and ample moisture. The soil utilized was collected from the secondary forest stands Qingyuan Forest CERN, containing  $80.4 \pm 4.2\ \text{g kg}^{-1}$  of total carbon,  $7.0 \pm 0.4\ \text{g kg}^{-1}$  of total nitrogen and  $1.1 \pm 0.2\ \text{g kg}^{-1}$  of total phosphorus (Zhang et al. 2022). These trays were placed in a translucent greenhouse in Shenyang (Institute of Applied Ecology, Chinese Academy of Sciences), and watered every 2 days to facilitate seedling emergence. In October 2021 (the end of the growing season), seedlings with similar root collar diameters ( $1.98 \pm 0.01\ \text{mm}$ ) and height ( $10.54 \pm 0.29\ \text{cm}$ ) were selected and then individually transplanted into pots with a diameter of 7.5 cm and a height of 17 cm, with one seedling per pot. To maintain an environment closer to natural conditions, the pots were moved to the understorey of the broad-leaved forest from October to February of the following year. The growing conditions in the understorey of a broad-leaved forest are shown in Supporting Information S1: Table S1 and Figure S1.

## 2.2 | Experimental Design

In March 2022, the pots were transferred to five incubators (MGC-450BP-2L, Shanghai Yiheng Scientific Instruments Co., Ltd., Shanghai, China), each featuring an internal space dimensioned at 0.70 m in length, 0.55 m in width and 1.14 m in height. These incubators were designed to simulate five temperature scenarios (Figure 1) with three categories: Category

I—(i) ‘control treatment (CK)’, representing the mean monthly day and night temperature of the Qingyuan Forest CERN during the growing season from 2005 to 2019; Category II—(ii) ‘SW’, simulating an increase of  $3^{\circ}\text{C}$  in both day and night mean temperature of CK; and Category III—asymmetric warming, including (iii) ‘DW’, simulating an increase of  $3^{\circ}\text{C}$  in the day mean temperature and no increase in mean night temperature of CK, (iv) ‘NW’, simulating an increase of  $3^{\circ}\text{C}$  in night mean temperature and no increase in mean day temperature of CK and (v) ‘DAW’, simulating an increase of  $2^{\circ}\text{C}$  in the day and  $4^{\circ}\text{C}$  in night mean temperature of CK. Weekly temperatures (day/night, in  $^{\circ}\text{C}$ ) of the study area (Qingyuan Forest CERN) during the 24-week experiment were recorded for the five temperature scenarios (Table 1). Each incubator housed 25 seedlings, totalling 125 seedlings across the five temperature treatments. The soil moisture in the pots was maintained at 41% (Yuan et al. 2022) by timely watering. For the whole experiment, light intensity in each incubator was constantly fixed at a photosynthetic photon flux density of  $12.5\ \mu\text{mol m}^{-2}\text{s}^{-1}$  for daytime, the light spectrum was between 400 and 700 nm and the light time was 10 h. All of these settings were consistent with real daytime irradiance levels and real light periods under the forest of the study area (Lu et al. 2018; Song et al. 2019). Supporting Information S1: Figure S2 provided a clear visualization of the monthly temperature, relative humidity (RH) and vapour pressure deficit (VPD) for the five treatments within the incubators. To eliminate potential chamber effects, seedlings were rotated among five distinct incubators every 10 days, with each seedling’s position randomized within its respective incubator (Matías et al. 2016).

At the end of the experiment (in late August 2022), we harvested all seedlings (25 seedlings) in each treatment. The 25 seedlings per treatment were divided into two groups,



**FIGURE 1** | A conceptual diagram that depicts the phenotypic characteristics of *Acer mono* seedlings under symmetric warming and asymmetric warming treatments, which includes diurnal asymmetric warming, day warming, and night warming. (a) control, (b) symmetric warming, (c) diurnal asymmetric warming, (d) day warming, and (e) night warming. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

**TABLE 1** | Weekly temperatures (day/night, in °C) of day or night during the experiment development in five temperature treatments

Week	Equivalent month	Phrase	Category I	Category II	Category III—Asymmetric warming		
			Control (CK)	Symmetric warming (SW)	Day warming (DW)	Night warming (NW)	Diurnal asymmetric warming (DAW)
			Monthly mean temperature	+3°C in both day and night	+3°C in day, and no warming in night	+3°C in night, and no warming in day	+2°C in day, and +4°C in night
1–4	March	Day	1.3	4.3	4.3	1.3	3.3
		Night	−0.2	2.8	−0.2	2.8	3.8
5–8	April	Day	6.8	9.8	9.8	6.8	8.8
		Night	4.2	7.2	4.2	7.2	8.2
9–12	May	Day	12.8	15.8	15.8	12.8	14.8
		Night	10.5	13.5	10.5	13.5	14.5
13–16	June	Day	17.7	20.7	20.7	17.7	19.7
		Night	14.5	17.5	14.5	17.5	18.5
17–20	July	Day	21.2	24.2	24.2	21.2	23.2
		Night	18.1	21.1	18.1	21.1	22.1
21–24	August	Day	18.0	21.0	21.0	18.0	20.0
		Night	15.1	18.1	15.1	18.1	19.1

Note: These values were obtained as monthly mean from the meteorological stations of Qingyuan Forest CERN during 2005–2019 series.

that is, one group consisted of 13 seedlings for dry sample, and the other group was composed of 12 seedlings for fresh sample. Each group was divided into four replicates, and each replicate contained three, three, three and four seedlings for dry samples and three seedlings for fresh samples. The dry sample was used to measure the leaf, stem and root biomass, and non-structure carbohydrate (NSC). The fresh sample was used to determine MDA and proline contents, SOD, peroxidase (POD) and AAO activity, and the levels of ABA and IAA.

### 2.3 | Phenology Measurements

All seedlings were utilized to investigate the impact of warming on maple phenology. Each seedling was monitored every 5 days before bud swelling and every 2 days after the initial observation of bud swelling. The top of the main branches of each seedling were selected for monitoring. The timing of each phenological stage was recorded from March to July 2022 and categorized into three stages: (1) the bud swelling date (marked by slightly split bracts and the presence of yellow-green or light green buds), (2) the budburst date (characterized by open buds and partially visible leaves, with the first appearance of the green leaf tip as the representative date for budburst), and (3) leaf unfolding date (marked by the full unfolding of the first leaf). The dates for each phenological stage were recorded when the corresponding feature was observed in 50% of the seedlings.

### 2.4 | Measurement of Growth Parameters

First, all seedlings were excavated, and the soil near the roots was carefully removed without causing damage. The final root collar diameter of the seedlings was then measured. To determine the maximum length of the roots, the roots were straightened from the stem's base to the tip of the root system, with the seedlings carefully positioned on a flat surface. The leaves of 13 seedlings for dry samples were promptly scanned using a digital scanner (Epson scanner). Subsequently, WinRhizo (Pro 2005b) analysis software was used to process the scanned images to calculate the leaf area. In each treatment, the dry sample of 13 seedlings were divided into leaves, stems and roots. These samples were then placed in an oven at 105°C for 20 min, followed by drying at 70°C for at least 72 h until obtaining a constant weight.

### 2.5 | Measurement of Physiological Parameters

We measured relative chlorophyll content (SPAD) at the phenological stage when leaves from five treatments were fully expanded (22 July 2022) (Li et al. 2023). The SPAD values were measured using a portable TYS-B chlorophyll metre (Topper, China). For each treatment, 10 representative seedlings were selected and marked for the measurements, with three fully developed current-year leaves per seedling being examined.

All dried samples were individually ground by components (leaf, stem and root) to pass a 0.25 mm mesh sieve for NSC

analysis. The anthrone-sulphuric acid method was used for measuring soluble sugar and starch. Each sample of 100 mg was extracted three times with 25 mL of 80% ethanol at 80°C for 30 min. The supernatants were pooled in a 100 mL volumetric flask and diluted with 85% ethanol to volume, then used to measure the amount of soluble sugar. To decompose the starch, the remaining sediments were boiled for 15 min after adding 2 mL of HClO<sub>4</sub>. Afterwards, 4 ml of distilled water was added, followed by centrifugation at 4000 rpm for 10 min. The supernatant was transferred to a 50 mL centrifuge tube. The sediment again was then extracted with distilled water and 2 ml HClO<sub>4</sub> solution. The amounts of soluble sugar and starch were determined spectrophotometrically at 620 nm using glucose as a standard. The NSC concentration was calculated as the sum of soluble sugar and starch in mg g<sup>-1</sup> dry mass.

The MDA content was measured using the thiobarbituric acid reaction method (Hodges et al. 1999). SOD activity was assessed following the method of Giannopolitis and Ries (1977). POD activity was determined using the lignin method referred to by Ekmekci and Terzioglu (2005). The free proline content was quantified in accordance with the method described by Bates et al. (1973). The ABA in leaves and IAA in root tips were detected with an Elisa kit (ZCIBIO Technology Co. Ltd) according to the vendor's instructions.

## 2.6 | Data Analysis

By measuring the dry biomass of roots, stems and leaves with a balance, we calculated the following biomass allocation parameters:

$$\text{Root mass ratio (RMR)} = \frac{\text{Root dry weight}}{\text{total dry weight}}, \quad (1)$$

$$\text{Stem mass ratio (SMR)} = \frac{\text{Stem dry weight}}{\text{Total dry weight}}, \quad (2)$$

$$\text{Leaf mass ratio (LMR)} = \frac{\text{Leaf dry weight}}{\text{Total dry weight}}, \quad (3)$$

$$\text{Root shoot ratio (R/S)} = \frac{\text{Belowground dry weight}}{\text{aboveground dry weight}}. \quad (4)$$

A one-way ANOVA with a post hoc multiple-comparison (least significant difference) test was used to examine the significant level of the differences in the parameters of phenology, growth, and physiology among the five temperature treatments. The significant differences under different treatments were tested at  $p < 0.05$  using the R version 4.3.1 (R Core Team, Vienna, Austria). Log transformation was used when necessary to achieve normality and homogeneity of variance. A car package (Fox et al. 2013) was used for normality tests and ANOVAs. Results were shown as mean  $\pm$  SE throughout the paper.

Principal component analysis (PCA) was conducted to explore and visualize the relationships between the multiple quantitative

metrics and to identify which metrics are the most crucial in distinguishing the functional differences among treatments. All indices of leaves and roots were included, while indices of stems were excluded. The five temperature treatments were considered as a categorical variable. Here, we used the package stats for the analysis and factoextra for ggplot2-based visualization (Kassambara and Mundt 2020). The scores of the variables in each temperature treatment were obtained through the score function and only selected the scores along the first two dimensions.

## 3 | Results

### 3.1 | Plant Phenology

Only DW and DAW significantly altered the dates of phenological events relative to the CK. Compared to the control, DW advanced the dates of bud swelling, budburst and leaf unfolding by 14.8, 16.8 and 15.5 days, respectively ( $p < 0.0001$ ; Table 2 and Supporting Information S1: Figure S3). Similarly, DAW advanced the dates of bud swelling, budburst and leaf unfolding by 15.5, 16.3 and 15.3 days, respectively ( $p < 0.0001$ ; Table 2 and Supporting Information S1: Figure S3). Additionally, compared to SW, DAW had advanced the dates of bud swelling and leaf unfolding by 9.25 and 10 days, respectively ( $p < 0.0001$ ; Table 2 and Supporting Information S1: Table S2 and Figure S3).

### 3.2 | Growth and Morphology of Seedlings

The root length of seedlings under DW, NW and SW was increased by 266.0%, 146.9% and 111.1%, respectively ( $p < 0.0001$ ; Table 2 and Figure 2a). The total leaf area under warming showed an increasing trend compared to CK ( $p < 0.05$ ; Table 2, Supporting Information S1: Table S2 and Figure 3a). DAW decreased the total leaf area by 20.1% compared to SW.

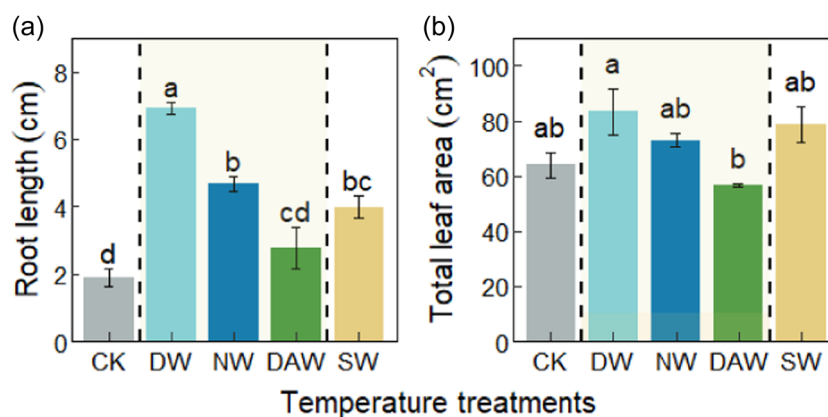
DW enhanced the growth of seedlings and DAW was more beneficial for the growth of seedlings than SW. Compared to CK, DW significantly enhanced leaf biomass by 52.5%, while SW reduced it by 58.0% ( $p < 0.0001$ ; Table 2, Supporting Information S1: Table S2 and Figure 3a). DAW increased leaf and stem biomass by 192.35% and 36.86%, respectively, compared to SW. Compared to CK, NW and SW significantly decreased stem biomass by 52.3% and 40.1%, respectively ( $p < 0.001$ ; Table 2, Supporting Information S1: Table S2 and Figure 3b). The root biomass under DW and DAW was significantly higher than that of CK ( $p < 0.05$ ; Table 2 and Figure 3c). While DW significantly increased total biomass by 38.1%. Compared to SW, DAW enhanced total biomass by 47.46% ( $p < 0.05$ ; Table 2, Supporting Information S1: Table S2 and Figure 3d).

Overall, warming enhanced the growth of roots, with SW having a more significant effect than asymmetrical warming. The leaf-to-mass ratio of SW was significantly lower than CK ( $p < 0.0001$ ; Table 2, Supporting Information S1: Table S2 and Figure 3e), while DAW had a higher leaf-to-mass ratio than SW. Similarly, warming reduced the stem-to-mass ratio, that is, the stem-to-mass ratios under NW and DAW were significantly

**TABLE 2** | Summary of statistics (*F* and *p* values).

	<i>F</i>	<i>p</i>		<i>F</i>	<i>p</i>
The date of bud swelling	29.23	< 0.0001	stem-to-mass ratio	4.652	<b>0.01</b>
The date of budburst	21.14	< 0.0001	root-to-mass ratio	15.36	< 0.0001
The date of leaf unfolding	21.73	< 0.0001	root-to-shoot ratio	11.97	< 0.0001
Root length	27.86	< 0.0001	Relative chlorophyll content	162.2	< 0.0001
Total leaf area	4.28	<b>0.02</b>	Indole-3-acetic acid content	12.72	< 0.0001
Leaf biomass	12.93	< 0.0001	Abscisic acid content	15.38	< 0.0001
Stem biomass	23.8	< 0.0001	Malonaldehyde content	25.86	< 0.0001
Root biomass	8.47	< 0.0001	Superoxide dismutase activity	54.88	< 0.0001
Total biomass	15.52	< 0.0001	Peroxidase activity	26.81	< 0.0001
leaf-to-mass ratio	8.70	< 0.0001	Proline content	131	< 0.0001

Note: Differences in phenology, growth and physiology parameters were tested by using factorial ANOVA (*F* values) across the different temperature treatments. Significant results ( $p < 0.05$ ) are shown in bold.



**FIGURE 2** | Effects of five temperature treatments on the root length ( $n = 4$ , cm) (a) and total leaf area ( $n = 4$ , cm<sup>2</sup>) (b) of *Acer mono*. Data are shown as mean  $\pm$  standard error. Different lowercase letters indicate the significant differences between different temperature treatments ( $p < 0.05$ ). CK, control; DAW, diurnal asymmetric warming; DW, day warming; NW, night warming; SW, symmetric warming. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

lower than that under CK ( $p < 0.05$ ; Table 2, Supporting Information S1: Table S2 and Figure 3f). Contrary to above-ground parts, warming increased the root-to-mass ratio and root-to-shoot ratio. Compared with CK, DAW, NW and SW significantly enhanced root-to-mass ratio ( $p < 0.0001$ ; Table 2, Supporting Information S1: Table S2 and Figure 3g), and NW and SW significantly enhanced root-to-shoot ratio ( $p < 0.0001$ ; Table 2, Supporting Information S1: Table S2 and Figure 3h). There was no difference in root-to-mass ratio between DAW and SW.

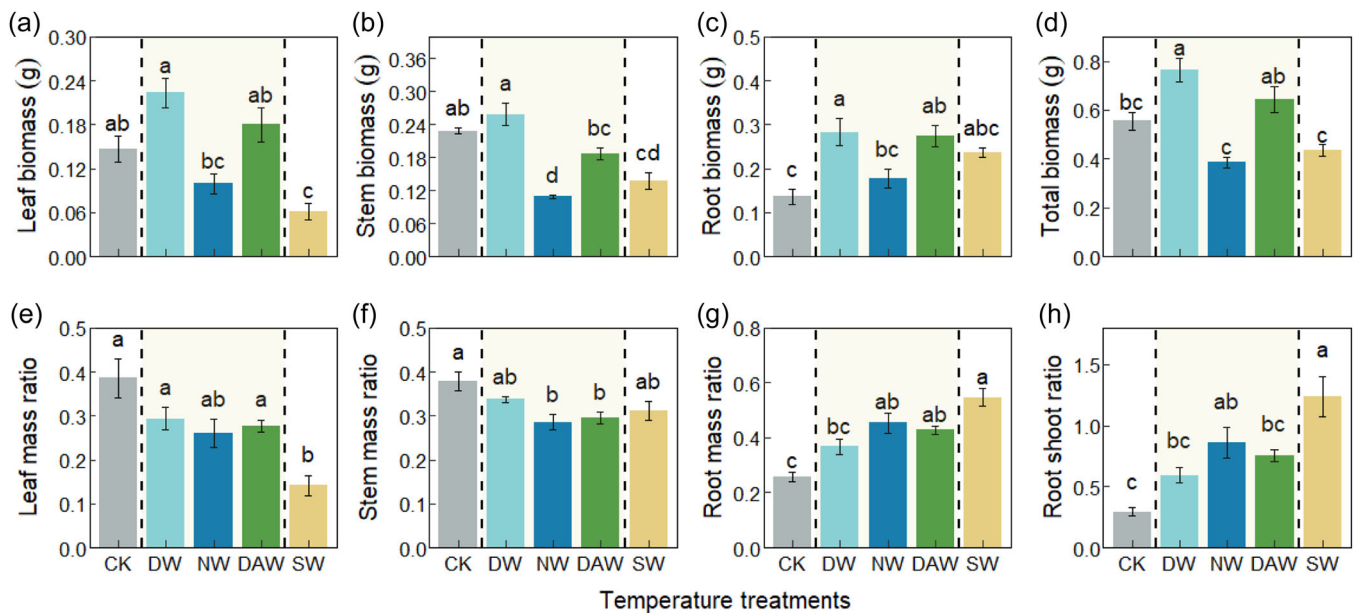
### 3.3 | Physiological Characteristics of Seedlings

Apart from DW, the other four warming treatments decreased the relative chlorophyll content. Compared with CK, DW significantly increased the relative chlorophyll content by 10.2%, while NW, DAW and SW reduced the relative chlorophyll content by 21.3%, 7.6% and 30.3%, respectively. Notably, the relative chlorophyll content of SW was the lowest among the five treatments ( $p < 0.0001$ ; Table 2, Supporting Information S1: Table S2 and Figure 4). Relative

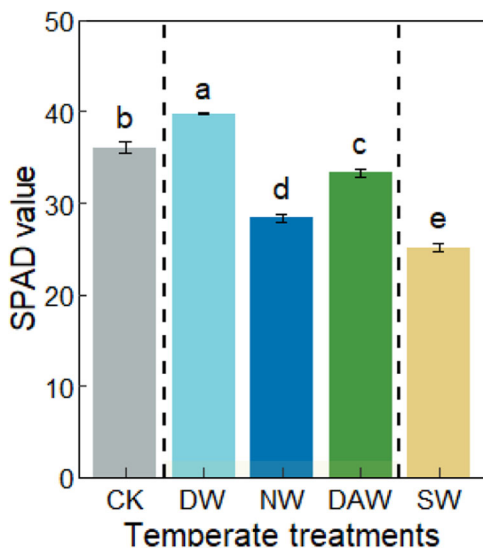
to SW, DAW increased the relative chlorophyll content by 32.5%.

Overall, DAW and SW promoted antioxidant enzyme activity and MDA content. DAW and SW significantly increased the MDA content of leaves by 48.5% and 46.4%, respectively ( $p < 0.0001$ ; Table 2 and Supporting Information S1: Table S2 and Figure S4a). In addition, DAW and SW had similar MDA content. Relative to CK, DW and SW significantly reduced SOD activity by 85.0% and 70.9%, respectively ( $p < 0.0001$ ; Table 2, Supporting Information S1: Table S2 and Figure S4b); DAW had a higher SOD activity compared to SW. DAW and SW significantly increased POD activity by 234.7% and 352.9%, respectively ( $p < 0.0001$ ; Table 2 and Supporting Information S1: Table S2 and Figure S4c). Similarly, DAW and SW significantly increased proline content by 116.6% and 91.6%, compared with CK ( $p < 0.0001$ ; Table 2 and Supporting Information S1: Table S2 and Figure S4d). DAW enhanced proline content by 13.07% relative to SW.

DAW significantly increased the IAA content in root tips and the ABA content in leaves. Warming increased the IAA content

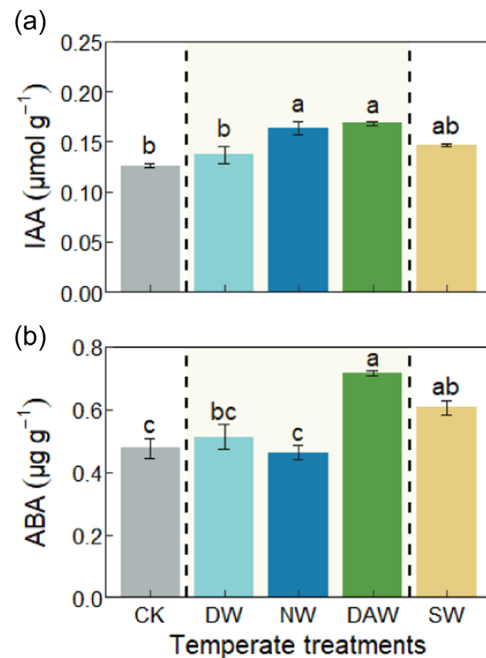


**FIGURE 3** | Effects of different temperature treatments on the leaf biomass ( $n = 4$ , g) (a), stem biomass ( $n = 4$ , g) (b), root biomass ( $n = 4$ , g) (c), total biomass ( $n = 4$ , g) (d), leaf-to-mass ratio ( $n = 4$ ) (e), stem-to-mass ratio ( $n = 4$ ) (f), root-to-mass ratio ( $n = 4$ ) (g) and root-to-shoot ratio ( $n = 4$ ) (h) of *Acer mono*. Data are shown as mean  $\pm$  standard error. Different lowercase letters indicate the significant differences between different temperature treatments ( $p < 0.05$ ). CK, control; DAW, diurnal asymmetric warming; DW, day warming; NW, night warming; SW, symmetric warming. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 4** | Effects of different temperature treatments on the relative chlorophyll content ( $n = 4$ , SPAD value) of *Acer mono*. Data are shown as mean  $\pm$  standard error. Different lowercase letters indicate the significant differences between different temperature treatments ( $p < 0.05$ ). CK, control; DAW, diurnal asymmetric warming; DW, day warming; NW, night warming; SW, symmetric warming. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

in root tips, that is, relative to CK, NW and DAW significantly increased it by 29.4% and 33.4%, respectively ( $p < 0.0001$ ; Table 2, Supporting Information S1: Table S2 and Figure 5a). Additionally, DAW increased the IAA content in root tips by 14.67%, compared to SW. Only DAW and SW significantly



**FIGURE 5** | Effects of different temperature treatments on the indole-3-acetic acid (IAA,  $n = 4$ ,  $\mu\text{mol g}^{-1}$ ) contents in root tips (a) and abscisic acid (ABA,  $n = 4$ ,  $\mu\text{g g}^{-1}$ ) content in leaves (b) of *Acer mono*. Data are shown as mean  $\pm$  standard error. Different lowercase letters indicate the significant differences between different temperature treatments ( $p < 0.05$ ). CK, control; DAW, diurnal asymmetric warming; DW, day warming; NW, night warming; SW, symmetric warming. [Color figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**TABLE 3** | Summary of statistics (*F* and *p* values).

	Root		Stem		Leaf	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
Soluble sugar concentration	3.49	<b>0.03</b>	13.97	<b>&lt; 0.0001</b>	3.00	0.05
Starch concentration	12.8	<b>&lt; 0.0001</b>	4.47	<b>&lt; 0.0001</b>	69.81	<b>&lt; 0.0001</b>
NSC concentration	12.51	<b>&lt; 0.0001</b>	9.15	<b>&lt; 0.0001</b>	27.66	<b>&lt; 0.0001</b>
The ratio of soluble sugar to starch	4.30	<b>0.02</b>	4.76	<b>0.01</b>	21.24	<b>&lt; 0.0001</b>

Note: Differences in concentrations of soluble sugar ( $n = 4$ ,  $\text{mg g}^{-1}$ ), starch ( $n = 4$ ,  $\text{mg g}^{-1}$ ), NSC ( $n = 4$ ,  $\text{mg g}^{-1}$ ) and the ratio of soluble sugar to starch of root ( $n = 4$ ), stem ( $n = 4$ ) and leaf ( $n = 4$ ) were tested by using factorial ANOVA (*F* values) across the different temperature treatments. Significant results ( $p < 0.05$ ) are shown in bold.

enhanced ABA content in leaves by 50.0% and 27.3%, respectively, compared to CK ( $p < 0.0001$ ; Table 2, Supporting Information S1: Table S2 and Figure 5b). Compared to SW, DAW increased IAA in root tips and ABA content in leaves by 14.67% and 17.89%, respectively.

The starch and NSC concentrations in the roots were lower for NW and SW treatments compared to CK. There was an increasing trend of the soluble sugar concentration in the root with warming ( $p < 0.05$ ; Table 3, Supporting Information S1: Table S3 and Figure 6a). Relative to CK, NW and SW significantly decreased starch concentration in the root by 32.9% and 31.8%, respectively ( $p < 0.0001$ ; Table 3, Supporting Information S1: Table S3 and Figure 6d). The NSC concentrations in the root of DW and DAW were greater than SW and NW ( $p < 0.0001$ ; Table 3, Supporting Information S1: Table S3 and Figure 6g). Relative to CK, NW, DAW and SW significantly enhanced the ratio of soluble sugar to starch in the root by 54.6%, 28.2% and 46.4%, respectively ( $p < 0.05$ ; Table 3, Supporting Information S1: Table S3 and Figure 6j). DAW increased the soluble sugar, starch and NSC concentration in the root by 30.52%, 49.21%, and 38.50%, respectively, compared to SW.

The lowest soluble sugar, starch and NSC concentration in the stem occurred in the DAW treatment. Relative to CK, DAW and SW significantly decreased soluble sugar concentration in stems by 29.6% and 26.8%, respectively ( $p < 0.0001$ ; Table 3, Supporting Information S1: Table S3 and Figure 6b). Only SW significantly decreased the ratio of soluble sugar to starch in the stem by 30.1% compared with CK ( $p < 0.05$ ; Table 3, Supporting Information S1: Table S3 and Figure 6k). In addition, DAW and SW had similar soluble sugar, starch and NSC concentration and the ratio of soluble sugar to starch in the stem.

The lowest NSC concentration in the leaf was observed in the NW treatment. Relative to CK, DAW and SW significantly enhanced starch concentration in the leaf by 62.7% and 70.1%, respectively, while NW significantly decreased it by 27.1% ( $p < 0.0001$ ; Table 3, Supporting Information S1: Table S3 and Figure 6f). Similarly, DAW and SW significantly enhanced NSC concentration in the leaf by 22.2% and 38%, respectively, while NW significantly decreased it by 23.9% ( $p < 0.0001$ ; Table 3, Supporting Information S1: Table S3 and Figure 6i). The ratio of soluble sugar to starch of DW and NW in the leaf was greater than SW and DAW. Similar to the stem, there was no variation in the concentrations of soluble sugar, starch and NSC, and the ratio of soluble sugar to starch in the root between DAW and SW.

### 3.4 | PCA of Growth and Physiological Parameters

The first two principal components (PCs; axes) of the PCA explained 59.7% of the variance in metrics of seedlings, with PC1 accounting for 33.9% and PC2 for 25.8% (Table 4 and Figure 7). The first dimension (PC1) was highly positively related to the changes in NSC and starch concentration of leaf, POD activity, starch concentration of leaf and root-to-shoot ratio, while the root length was negatively correlated with the first dimension. However, the second dimension (PC2) was positively linked to the NSC and starch concentration in the root and dry weight of the root, and negatively associated with total leaf area. Furthermore, the highest score was for DW, followed by CK, DAW and NW, and the lowest score was for SW (Table 5 and Figure 7).

## 4 | Discussion

### 4.1 | Phenological, Growth, and Physiological Response to DW

DW significantly advanced the dates of bud swelling, budburst and leaf unfolding, attributed to positive responses to day temperature for bud break (Rossi and Isabel 2016). In line with our findings, Piao et al. (2015) demonstrated that advanced phenology in the northern hemisphere was mainly triggered by increasing day temperature rather than night temperature, indicating an extended period of active plant growth under asymmetric warming conditions. This phenomenon can potentially stem from two distinct factors. First, the interaction between photoperiod and daytime temperature in the early spring season might amplify the correlation with daytime temperature. Second, given that the majority of plant photosynthesis takes place during daylight hours and ceases during the night, daytime temperature becomes a more pivotal determinant for plant carbon fixation and energy capture, thereby exerting a more profound influence on the onset of spring phenology than nighttime temperature (Piao et al. 2015). Moreover, advanced phenology may lead to mismatches with seed dispersers, pollinators and herbivores (Amico et al. 2022; Ekholm et al. 2022), as well as changes in competition among different species (Dumandan et al. 2023). The growth of seedlings benefited from DW due to higher photosynthesis caused by increasing chlorophyll content (Tan et al. 2014; Du et al. 2019), which was consistent with our first hypothesis.



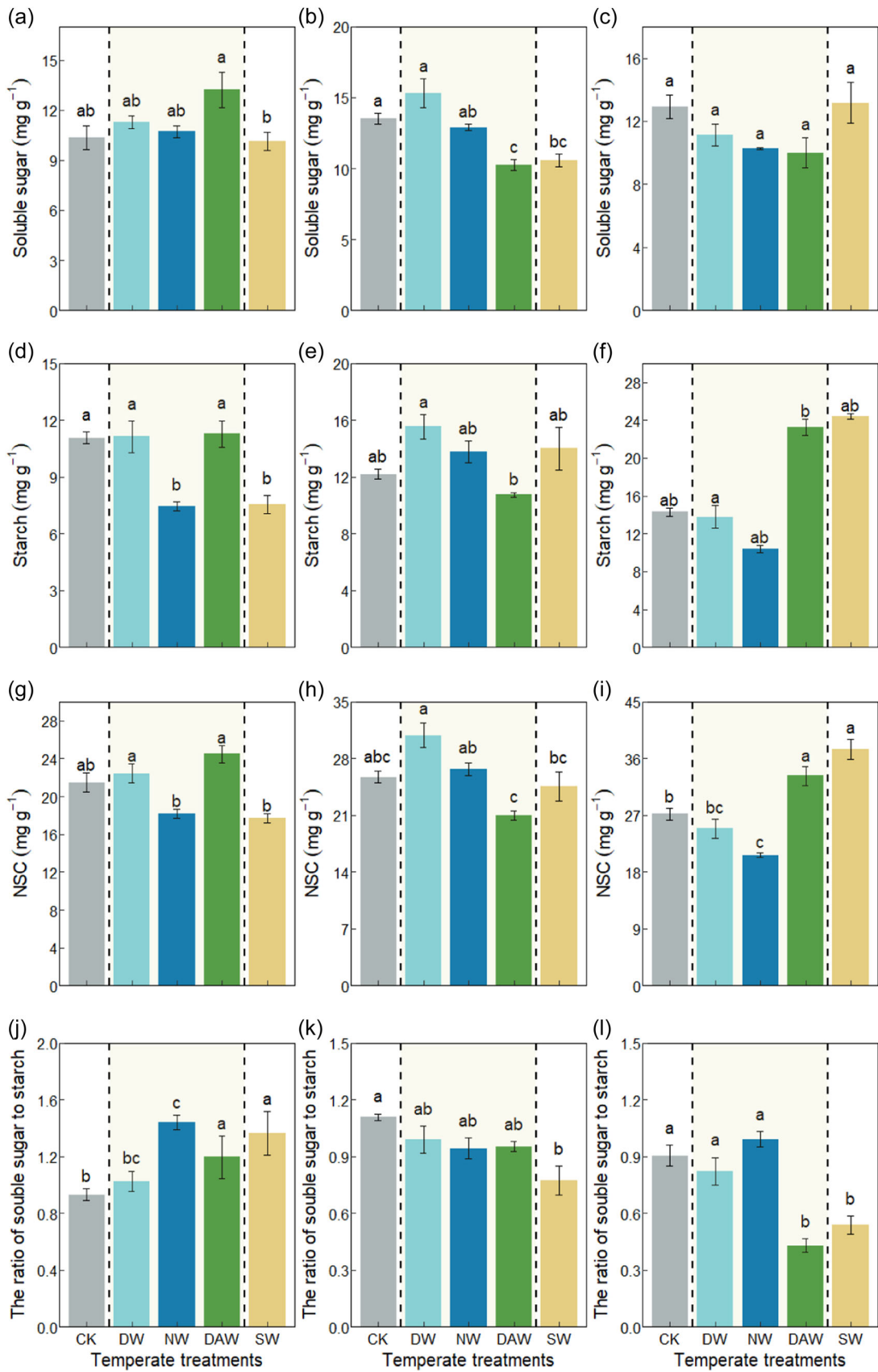


FIGURE 6 | Legend on next page.

**TABLE 4** | Eigenvalue, variance contribution rate, cumulative contribution rate and component load matrix of principal components.

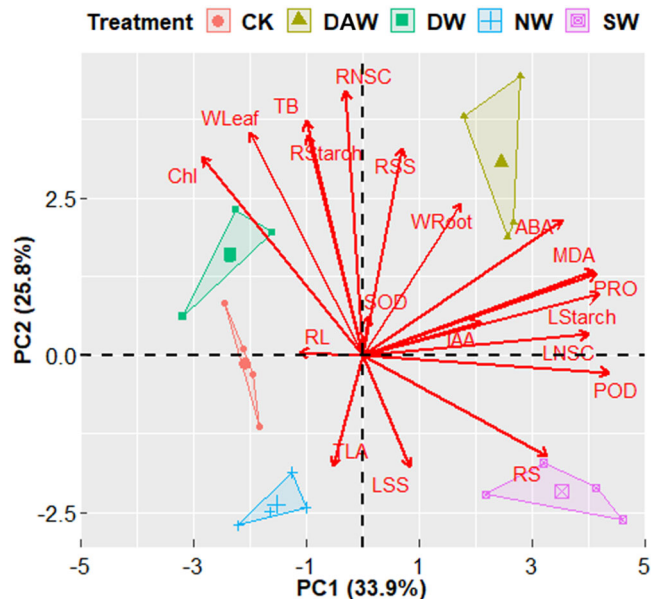
Variables	Principal component	
	Prin 1	Prin 2
RL	-0.25	0.01
TLA	-0.12	-0.39
WLeaf	-0.44	0.78
WRoot	0.38	0.53
TB	-0.22	0.82
RS	0.72	-0.35
Chl	-0.63	0.69
SOD	0.02	0.13
POD	0.95	-0.06
MDA	0.90	0.30
PRO	0.91	0.29
RSS	0.15	0.72
LSS	0.18	-0.39
RStarch	-0.22	0.77
LStarch	0.92	0.22
RNSC	-0.07	0.92
LNSC	0.88	0.07
ABA	0.78	0.47
IAA	0.46	0.12
Eigenvalue	6.44	4.91
Percent (%)	33.87	25.82
Cumulative percent (%)	33.87	59.70

Abbreviations: ABA, abscisic acid; Chl, relative chlorophyll content; IAA, indole-3-acetic acid; LNSC, concentration of non-structural carbohydrate in leaf; LSS, concentration of soluble sugar in leaf; LStarch, concentration of starch in leaf; MDA, malonaldehyde; POD, peroxidase; RL, root length; RNSC, concentration of non-structural carbohydrate in root; RS, root-to-shoot ratio; RSS, concentration of soluble sugar in root; RStarch, concentration of starch in root; SOD, superoxide dismutase; TB, total biomass; TLA, total leaf area; WLeaf, dry weight of leaf; WRoot, dry weight of root.

## 4.2 | Phenological, Growth, and Physiological Responses to NW

We found that NW reduced stem biomass, which might be driven by elevated respiration under increased night temperatures (Cheesman and Winter 2012). Consistent with our results, prior studies have also noted a positive correlation between respiration and stem dry weight (Cheng et al. 2009). Additionally, NW decreased chlorophyll content, resulting in reduced photosynthesis, which further inhibited carbohydrate accumulation and plant growth (Pakharkova et al. 2020; Sonti

**FIGURE 6** | Effects of different temperature treatments on the concentration of soluble sugar ( $n = 4$ ,  $\text{mg g}^{-1}$ ) (a), starch ( $n = 4$ ,  $\text{mg g}^{-1}$ ) (d), non-structural carbohydrate ( $n = 4$ ,  $\text{mg g}^{-1}$ ) (NSC) (g) and ratio of soluble sugar to starch ( $n = 4$ ) (j) in roots, the concentration of soluble sugar ( $n = 4$ ,  $\text{mg g}^{-1}$ ) (b), starch ( $n = 4$ ,  $\text{mg g}^{-1}$ ) (e), NSC ( $n = 4$ ,  $\text{mg g}^{-1}$ ) (h) and ratio of soluble sugar to starch ( $n = 4$ ) (k) in stems, and the concentration of soluble sugar ( $n = 4$ ,  $\text{mg g}^{-1}$ ) (c), starch ( $n = 4$ ,  $\text{mg g}^{-1}$ ) (f), NSC ( $n = 4$ ,  $\text{mg g}^{-1}$ ) (i) and ratio of soluble sugar to starch ( $n = 4$ ) (l) in leaves of *Acer mono*. Data are shown as mean  $\pm$  standard error. Different lowercase letters indicate the significant differences between different temperature treatments ( $p < 0.05$ ). CK, control; DAW, diurnal asymmetric warming; DW, day warming; NW, night warming; SW, symmetric warming. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]



**FIGURE 7** | Principal component analysis (PCA) for growth and physiological traits for seedlings from five temperature treatments for the first two axes. Trait abbreviations are the same as those in Table 4. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.com)]

**TABLE 5** | Overall score of growth and physiological parameters for different temperature treatments.

Treatments	PC1 scores	PC2 scores	Scores
CK	8.13	-0.49	3.82
DW	9.16	6.24	7.70
NW	5.97	-9.24	-1.64
DAW	-9.54	11.93	1.19
SW	-13.72	-8.43	-11.08

Abbreviations: CK, control; DAW, diurnal asymmetric warming; DW, day warming; NW, night warming; SW, symmetric warming.

et al. 2021; Approbato et al. 2023). Contrary to our finding, Wan et al. (2009) demonstrated that NW (around  $+1^{\circ}\text{C}$ ) consequently increased photosynthesis by 19.8% in the subsequent days. This discrepancy may be due to the higher night temperature ( $+3^{\circ}\text{C}$ ) in our study, leading to a more pronounced increase in respiration. These findings did not support our second hypothesis that NW promoted growth due to compensatory photosynthesis. The higher levels of IAA achieved through NW could promote root growth, enhancing the uptake of water and nutrients (Wang et al. 2020). Moreover, a higher ratio of soluble sugar to starch in the root could induce a higher osmotic potential, facilitating increased water and nutrient absorption (Sun et al. 2022). Although warming induced a slight

decrease in soil moisture during the experiment, the sensitivity of *A. mono* seedlings to water likely contributed to the promotion of root growth (Zhao et al. 2022). In addition, our observations showed that warming treatments led to increased root length and root-to-mass ratio for *A. mono* seedlings, suggesting that these seedlings under warming allocated more biomass to belowground growth. This finding is supported by other studies (Zhou et al. 2022; Chandregowda et al. 2023). Notably, the allocation of more biomass to roots under warming conditions emerges as a crucial strategy for efficient water and nutrient absorption (Chandregowda et al. 2022, 2023).

### 4.3 | Phenological, Growth and Physiological Responses to DAW

Compared to CK, DAW significantly advanced the dates of bud swelling, budburst and leaf unfolding, similar to most effects observed under asymmetric warming, which supports our third hypothesis. This indicates that DAW may surpass the chilling threshold required for the spring phenology of *A. mono*. DAW decreased the diurnal temperature range and was more in line with the actual warming scenario than SW. Our results showed that DAW increased the root biomass without significant variation in total biomass compared to CK. This augmentation in root biomass could promote nutrient and water uptake, representing a critical adaptive strategy for plant survival in a stressful environment (Madouh 2022; Liao et al. 2020). Elevated SOD and POD activity, along with increased MDA and proline content, suggest that *A. mono* seedlings experienced stress. Consequently, *A. mono* seedlings have the potential to adapt to DAW by increasing the leaf thickness and number of cells in the leaves while reducing the total leaf area. Moreover, higher ABA content under asymmetric warming triggered stomatal closure to reduce water loss and respiration. Increased starch levels in leaves also helped *A. mono* seedlings tolerate heat stress. In summary, DAW demonstrated no significant impact on the growth of *A. mono*. However, we acknowledge the importance of understanding the physiological regulatory mechanisms of DAW on growth, which requires precise measurements of leaf thickness, cell count and stomatal closure patterns in future experiments.

### 4.4 | Differences in Symmetric and Asymmetric Warming Effects on Phenological, Growth and Physiological Responses of Seedlings

Compared to SW, DAW advanced the dates of bud swelling and leaf unfolding, likely due to reduced frost damage associated with NW (Shen et al. 2018), consistent with our third hypothesis. Similarly, Kreyling et al. (2019) observed that advanced phenology accounted for the increased aboveground biomass production under asymmetric warming conditions. Our results showed that DAW significantly enhanced the aboveground biomass (leaf and stem), total biomass and NSC concentration in roots relative to SW. As expected, DAW promoted seedling growth of *A. mono* by enhancing chlorophyll content relative to symmetric warming. The higher NSC concentration in the root was conducive to absorbing water and nutrients, promoting the

growth of seedlings (Duan et al. 2023; Guo et al. 2024). In addition, decreased ABA content in the leaves might inhibit respiration and thus enhance the growth of aboveground parts (Mohammed et al. 2013). Therefore, models based on symmetric warming might underestimate plant growth and carbon sequestration under real warming conditions. Furthermore, since only one species (species' level) was measured in this study due to manpower constraints and the limitation of incubator space, caution is needed when generalizing these results to mixed-species forests. Furthermore, there exist significant differences between the growth environments and physiological states of seedlings and mature plants, and biomass allocation is dependent on the balance between photosynthetic gains and respiratory losses among plant parts (Poorter et al. 2012). According to the PCA results of the present study, DAW mainly increased root biomass while SW decreased leaf biomass. This may be explained by the increase in the ABA content of seedlings by DAW, because higher ABA contents of leaf may reduce leaf area and increase root biomass accumulation (Lovelli et al. 2012). Consequently, research results based on seedlings may not accurately reflect the true carbon sequestration of tree species. Moreover, the timescale of seedling research is often relatively short, which prevents a comprehensive assessment of the long-term effects of carbon sequestration.

## 5 | Conclusion

We provided experimental evidence indicating that phenology, physiology and growth of *A. mono* seedlings respond differentially to non-uniform diurnal warming. We found that (a) DW significantly promoted the growth of *A. mono* attributed to advanced phenology and increased chlorophyll content; (b) NW reduced chlorophyll content, leading to decreased stem growth and leaf NSC concentrations; and (c) DAW increased NSC concentrations in root and growth compared to SW, attributing to higher chlorophyll content and advanced phenology. *A. mono* might narrow down its distribution range in response to future warming conditions because the performance of *A. mono* seedlings under DAW appears to be inferior to the control.

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### Conflicts of Interest

The authors declare no conflicts of interest.

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### **Supporting Information**

Additional supporting information can be found online in the Supporting Information section.