

# Divergent responses of phenology and growth to summer and autumnal warming

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## Abstract

Plant phenology is highly sensitive to climate change, and shifts in autumnal foliar senescence are critical for plant productivity and nutrient cycling. Global warming has delayed the timing of foliar senescence, but the response of autumnal foliar senescence to nonuniform seasonal warming remains poorly understood, with experimental evidence in trees especially scarce. We therefore conducted a field experiment on seasonally asymmetric warming on 2-year-old larch (*Larix principis-rupprechtii*) seedlings in two hydrologically contrasting years (wet 2018 and dry 2019). Autumnal and year-round warming significantly delayed the timing of foliar senescence by 6 and 7 d in 2018, the wet year, with corresponding temperature sensitivities of  $6.73 \pm 1.47$  and  $8.26 \pm 1.00$  d/°C, respectively. Interestingly, the dates of senescence did not change across the warming treatments in 2019, the dry year. However, there was no significant effect of summer warming on the timing of foliar senescence neither in the wet nor dry year. The delayed autumnal foliar senescence was responsible for an increase in biomass only in the wet year, 2018. In contrast, summer warming, but not autumnal warming, increased the mortality of the seedlings in both 2018 and 2019. These results suggest that the hydrological conditions substantially modify the response of autumnal phenology and growth to seasonal warming. Autumnal warming increases growth, whereas summer warming could cause carbon starvation/hydraulic failure, reduce growth, and lead to higher mortality. Our results suggest that the functioning, ecosystem services, and sustainability of forests in the future depend on the strength and pattern of nonuniform seasonal warming. This study can inspire new research in phenology and tree growth in experiments with asymmetric warming.

## KEYWORDS

autumnal phenology, climate change, mortality, open-top chamber, productivity, seasonal warming

## 1 | INTRODUCTION

The surface air temperature over land during 2006–2015 has increased by 1.53°C since the period 1850–1900 and is predicted to increase further (IPCC, 2019). Global warming has greatly influenced ecosystem processes (Peñuelas et al., 2017; Peñuelas & Filella, 2001; Piao et al., 2008, 2010). Warming is however not seasonally uniform

and substantial asymmetric seasonal warming has been reported not only for high latitudes but also for temperate regions (Piao et al., 2010). The difference in responses of ecosystem processes to warming may thus be substantial across seasons (Estrella & Menzel, 2006; Neumann et al., 2017; Xia et al., 2014; Yan et al., 2020; Zohner & Renner, 2019). However, experimental evidences on the impact of asymmetric warming from tree species are dramatically limited.

Observational and experimental studies have demonstrated that plant phenology is highly sensitive to climate change, particularly under scenarios of warming (Fu et al., 2013; Piao et al., 2019; Yan et al., 2020). Changes in plant phenology (e.g., leaf unfolding and foliar senescence) alter the length of the growing season, with consequent influence on ecosystem structure and functioning (Peñuelas et al., 2009; Piao et al., 2007; Vitasse et al., 2009), such as plant productivity (Fridley, 2012; Gunderson et al., 2012; Piao et al., 2008) and carbon and nutrient cycling (Estiarte & Peñuelas, 2015; Keenan et al., 2014; Piao et al., 2007; Yan et al., 2016). Autumnal events are of great ecological and evolutionary importance (Fridley, 2012; Fu et al., 2018; Yan et al., 2017, 2018), but the impacts of climate change on autumnal phenology have received less attention compared with spring phenology (Gallinat et al., 2015; Piao et al., 2019; Zohner et al., 2019). Previous studies have found that foliar phenology is more sensitive to temperature in autumn than spring (Fu et al., 2018; Han et al., 2014) and that sensitivity of autumnal phenology to temperature plays an even more important role in regulating plant productivity (Fridley, 2012; Keenan et al., 2014; Wu et al., 2013) and the length of the growing season than the temperature sensitivity of spring phenology (Jeong et al., 2011; Marchin et al., 2015). In addition, current knowledge of autumnal phenology has mainly been derived from long-term ground-based observations or remotely sensed data (Chen et al., 2020; Liu et al., 2016; Wu et al., 2018; Xie et al., 2018), whereas *in situ* manipulative experiments are much less common due to their cost and practical reasons (Fu et al., 2018; Richardson et al., 2018).

The response of autumnal foliar senescence to warming in deciduous trees is highly variable, for example, with significantly delayed responses (Fu et al., 2018; Richardson et al., 2018), advanced responses (Estrella & Menzel, 2006), or no response (Morin et al., 2010). Previous studies have associated the most pronounced delay of autumnal foliar coloring and abscission with increased temperatures in late summer (Fu et al., 2018), early autumn (Estrella & Menzel, 2006), or late spring (Menzel et al., 2008). That is, warming in different seasons may have varied impacts on autumnal foliar senescence (Estrella & Menzel, 2006). This is probably due to the variability of the dominant ecophysiological processes affected by nonuniform seasonal warming (Fu et al., 2018; Xia et al., 2014; Zani et al., 2020). More experimental evidence is therefore needed to elucidate the effects of nonuniform seasonal warming on foliar senescence and to improve our ability to predict the responses of plant autumnal phenology and productivity to scenarios of future climatic warming (Yu et al., 2010).

Experimental warming studies on autumnal phenology have commonly been conducted using pot experiments in temperature-controlled chambers (Fu et al., 2018; Zohner & Renner, 2019). Therefore, evidence from field experiments may provide more insights into the responses of plant phenology to climate changes (Signarbieux et al., 2017). The effects of warming on ecosystem processes, including phenology (Ganjurjav et al., 2020), are also often confounded by the availability of water (Reich et al., 2018). However, how the availability of water mediates the responses of phenology to seasonal warming in tree species remains unclear, particularly in experimental studies.

We performed a nonuniform seasonal-warming field experiment using open-top chambers in two hydrologically contrasting years (a wet 2018 and a dry 2019) to assess the responses of autumnal foliar senescence and growth of seedlings of a larch species (*Larix principis-rupprechtii*) to seasonally asymmetric warming. Larches (*Larix* spp.) are the most popular conifer species and extensively distributed in the temperate Northern Hemisphere. Specifically, we tested the hypotheses: (i) warming would delay autumnal foliar senescence and stimulate the productivity of larch seedlings due to that warming can delay the degradation of chlorophyll and alleviate low temperature constraints on growth (Fracheboud et al., 2009; Fu et al., 2018) and (ii) the magnitude and sensitivity of the response of foliar senescence to nonuniform seasonal warming would vary with the seasonal exposure, as warming can differentially influence the dominant ecophysiological process among seasons (Fu et al., 2018; Xia et al., 2014).

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The experiment was conducted at the Saihanba Ecological Station of Peking University (42°24.723'N, 117°14.844'E; 1505 m a.s.l.) in the Saihanba National Forest Park in Hebei Province in northern China. The climate is semi-humid and characterized by long and cold winters (November–March) and short springs and summers. The long-term (1969–2019) mean annual temperature and precipitation are −1.0°C and 460 mm, respectively. The topography is relatively flat, and the soil is mainly sandy. Snow begins to fall in mid-October and melts in early April, with accumulation less than 30 cm.

### 2.2 | Experimental design

Healthy, similarly sized ( $45.55 \pm 6.09$  cm in height and  $4.48 \pm 0.59$  mm in basal diameter) 2-year-old seedlings of *Larix principis-rupprechtii* were transplanted from a local nursery to the field in early May 2018. The experiment had a completely randomized design. Six warming treatments were applied and randomly allocated to each of the six blocks, with six replicate plots for each treatment, for a total of 36 plots subjected to nonuniform seasonal warming. In all, 12 seedlings were transplanted to each plot. Hexagonal open-top chambers (OTCs) were used to simulate warming. Each chamber was 0.92 m high, 1.69 m long at the bottom, and 1.15 m long at the top and was constructed using transparent polymethyl methacrylate (Figure S1). The nonuniform seasonal warming treatments were as follows: a control (without OTC warming), spring warming (with OTC warming from 20 February to 19 May), summer warming (with OTC warming from 20 May to 19 August), autumnal warming (with OTC warming from 20 August to 19 November), winter warming (with OTC warming from 20 November to 19 February), and year-round warming (with OTC warming throughout the year).

The summer-warming treatment was initiated on 3 June 2018, the first year of the experiment. This experiment only used the control, summer-warming, autumnal-warming, and year-round warming treatments because of no exposure of autumnal phenology in spring and winter warming in 2018.

## 2.3 | Phenological monitoring

The timing of foliar senescence was recorded visually from August to October in 2018 and 2019 when the leaves changed color from green to yellow, we recorded the percentage (i.e., 5, 25, 50, 75, and 100%) of yellow leaves for each seedling at 2 d (early autumn) to 5 d (late autumn) intervals in the morning (09:00–11:00 local time). The dates when 5, 50, and 100% of the needles of each seedling had changed color from green to yellow were defined as the onset (the initiation of the process), the timing (the peak of the process, which depends on both the initiation and rate of the process), and the completion (the end of the process) of foliar senescence, respectively. The time from the onset to completion was defined as the duration of senescence.

## 2.4 | Ancillary meteorological and growth measurements

Air temperature ( $T_a$ , °C), relative air humidity (RH, %, 30 cm above the ground, with the sensor shielded from solar radiation), soil temperature (°C), and soil-water content ( $\text{m}^3/\text{m}^3$ , at a depth of 5 cm) were recorded every 30 min using a HOBO H21 Micro Station Data Logger (Onset Computer Corporation, Bourne, USA). The sensors were installed in the centers of the control or OTC plot. Vapor-pressure deficit (VPD, kPa) was calculated as follows:

$$\text{VPD} = 0.611 \times \exp\left(\frac{17.502T_a}{T_a + 240.970}\right) \times (1 - \text{RH}). \quad (1)$$

The sensitivity of foliar senescence to temperature ( $d/^\circ\text{C}$ , i.e., the change in days of the phenological event per °C change in air temperature between treatments) was calculated as the difference in the timing of foliar senescence (d) divided by the difference in air temperature (°C) between the warming and control treatments.

We randomly selected eight individuals of the transplanted seedlings from the nursery in early May 2018 to measure their basal diameters and total biomass. We developed the following equation to calculate the total biomass of the experimental seedlings in 2018 and 2019:

$$y = 3.1683 \times \exp(0.132x), \quad (2)$$

where  $y$  and  $x$  represent total biomass (in g) and basal diameter (in mm), respectively.

We measured the basal diameter of each seedling in each plot at both the beginning and end of the growing seasons. The relative increase (RI, %) in total biomass was calculated as follows:

$$\text{RI} = \frac{\text{Value}_{\text{end}} - \text{Value}_{\text{beginning}}}{\text{Value}_{\text{beginning}}} \times 100, \quad (3)$$

where  $\text{Value}_{\text{end}}$  and  $\text{Value}_{\text{beginning}}$  represent the total biomass at the end and beginning of the growing season, respectively.

Seedling mortality (M, %) was calculated as follows:

$$M = \frac{\text{Survival}_{\text{beginning}} - \text{Survival}_{\text{end}}}{\text{Survival}_{\text{beginning}}} \times 100,$$

where  $\text{Survival}_{\text{end}}$  and  $\text{Survival}_{\text{beginning}}$  represent the number of seedlings alive at the end and beginning of the growing season, respectively.

## 2.5 | Hydrologically contrasting years during the experiment (wet 2018 vs dry 2019)

The monthly mean air temperatures were similar in the two growing seasons, that is, 11.3 and 11.2°C in 2018 and 2019, respectively. However, monthly mean precipitation was significantly higher in 2018 (615.3 mm) than in 2019 (368.4 mm), particularly from June to September (Figure 1a). We took advantage of the contrasting hydrological conditions in these two experimental years (Figure 1b) by exploring the effect of the interaction between warming and the hydrological conditions on phenology and growth.

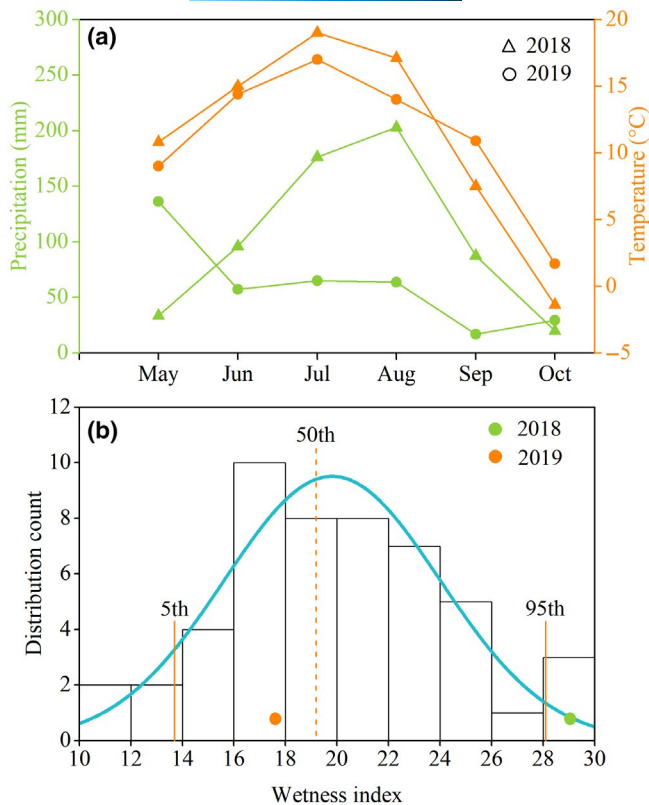
## 2.6 | Statistical analysis

The target variables (the timing of foliar senescence, growth, and mortality) were averaged for all individuals in each chamber. 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 timing of foliar senescence (also including onset and duration), seedling mortality, and RI in total biomass among the seasonal-warming treatments in 2018 and 2019. Nonparametric tests were used when needed. A paired-sample *t*-test was used to identify differences in the timing of foliar senescence, RI in total biomass, and seedling mortality in each warming treatment between 2018 and 2019. An independent-sample *t*-test was used to identify differences in the sensitivity of autumnal foliar senescence to temperature between autumnal and year-round warming in 2018. All statistical analyses were performed using SPSS 13.0 for Windows (SPSS, Inc., Chicago, USA). Differences were considered significant at  $p < 0.05$ .

# 3 | RESULTS

## 3.1 | Meteorological conditions between the control and warming treatments

Soil temperature, air temperature, and VPD increased by an average of 1.15°C, 0.85°C, and 0.03 kPa, respectively, and soil-water content decreased by an average of 0.0039  $\text{m}^3/\text{m}^3$ , in the year-round



**FIGURE 1** Monthly mean precipitation (mm) and air temperature (°C) during the growing season in 2018 and 2019 (a). Distribution of the wetness index (WI) during the growing seasons (May–October) from 1969 to 2019 at the study site, except for 1974 due to incomplete data (b). 5th, 50th, and 95th represent 5%, median, and 95% of the WI distribution, respectively.  $WI = P / (T + 10)$ . P and T represent total precipitation and mean air temperature during the growing season, respectively. A higher WI indicates wetter conditions

warming treatment compared to the control throughout the experiment, that is, from 3 June 2018 to 11 October 2019 (Figure 2).

Warming in 2018 (from 3 June to 11 October) and 2019 (from 20 May to 11 October) increased soil temperature by 0.81 (0.90 and 0.68°C in summer and autumnal warming, respectively) and 1.25 (0.54 and 2.48°C in summer and autumnal warming, respectively) °C, air temperature by 0.84 (0.87 and 0.80°C in summer and autumnal warming, respectively) and 1.12 (1.13 and 1.11°C in summer and autumnal warming, respectively) °C, and VPD by 0.0449 (0.0617 and 0.0202 kPa in summer and autumnal warming, respectively) and 0.0456 (0.0275 and 0.0770 kPa in summer and autumnal warming, respectively) kPa and decreased soil-water content by 0.0046 (0.0029 and 0.0071 m<sup>3</sup>/m<sup>3</sup> in summer and autumnal warming, respectively) and 0.0100 (0.0110 and 0.0084 m<sup>3</sup>/m<sup>3</sup> in summer and autumnal warming, respectively) m<sup>3</sup>/m<sup>3</sup>.

### 3.2 | Response of foliar senescence to nonuniform seasonal warming

Autumnal and year-round warming in the wet 2018 significantly delayed autumnal foliar senescence (50% coloration) by 6 and 7 d,

respectively, whereas summer warming did not delay the timing of foliar senescence (50% coloration) but delayed its onset (5% coloration), as did autumnal warming, by 4 and 5 d, respectively, relative to the control treatment (Figures 3a and 4, Table S1 in the appendix containing supplementary information). Interestingly, senescence in the dry 2019 was not significantly affected by any of the seasonal-warming treatments (Figure 3b). The duration of senescence (from the onset to completion) did not differ significantly between the warming treatments and the control, even though senescence was delayed (Figure 4; Table S1).

Foliar senescence in the control treatment was significantly advanced by 5 d in the dry 2019 compared to the wet 2018 (marginally significant at  $p = 0.077$ , Figure 3), and the dates of senescence in the year-round and autumnal-warming treatments were significantly advanced by 10 and 12 d, respectively.

### 3.3 | Responses of the temperature sensitivity of senescence, relative growth rate, and mortality of seedlings to warming

The sensitivity of foliar senescence to temperature in 2018 was not significantly different in the treatments with autumnal and year-round warming ( $6.73 \pm 1.47$  and  $8.26 \pm 1.00$  d/°C, Figure S2). The relative rate of increase (RI) in total biomass in 2018 was 5.65 and 3.51% higher in the autumnal- and year-round warming, respectively, compared with that in the control plots (Figure 5a; both  $p < 0.05$ ). In contrast, the RI in total biomass did not differ among the warming treatments in 2019.

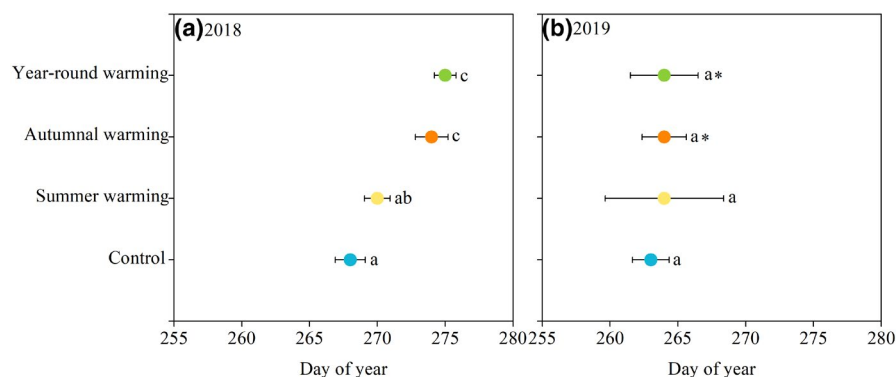
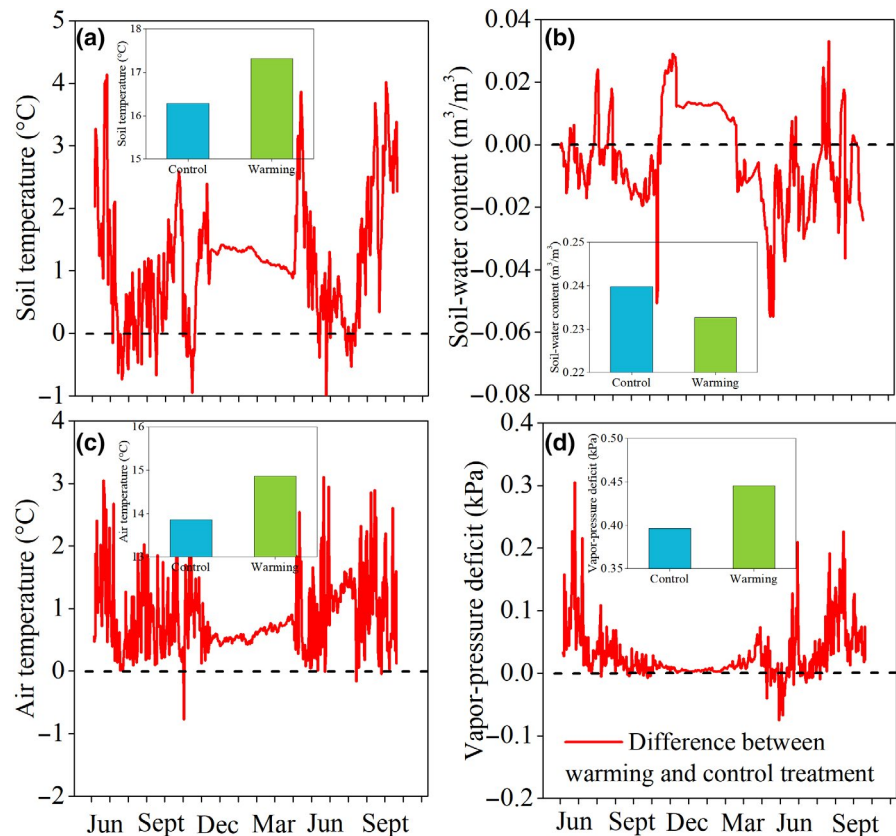
Seedling mortality was significantly higher (16.7 and 20.8% in 2018, and 72.2 and 30.6% in 2019) in the summer warming and year-round warming treatments than in the control treatment in both 2018 and 2019. Importantly, seedling mortality induced by summer warming was significantly higher in 2019 than 2018 (Figure 5b).

## 4 | DISCUSSION

### 4.1 | Later foliar senescence under autumnal warming

Our observations of delayed foliar senescence under the autumnal and year-round warming treatment are partly consistent with our first hypothesis and probably due to the activity of photosynthetic enzymes that could be maintained at a higher level under warmer conditions in autumn. The degradation rate of chlorophyll would likely decrease, and the timing of foliar senescence would thus be delayed (Fracheboud et al., 2009; Gunderson et al., 2012; Shi et al., 2015). In 2018, the relative changes in air temperature induced by warming treatment were largest among environmental factors, whereas environmental factors were more moderate in autumn relative to summer, suggesting that the delay in autumnal foliar senescence was probably mainly driven by the rise of autumnal air temperature. We found that summer warming did not significantly affect the

**FIGURE 2** Differences in mean daily soil temperature (a) and soil-water content at a depth of 5 cm (b), and air temperature (c), and vapor-pressure deficit (d) at 30 cm above the soil surface between the year-round warming and control treatments from 3 June 2018 to 11 October 2019. The dashed lines indicate no difference between the warming and control treatments for each meteorological variable. Insets show the absolute means of each climatic variable for the control (blue bars) and warming (green bars) treatments from 3 June to 11 October in 2018 and 2019

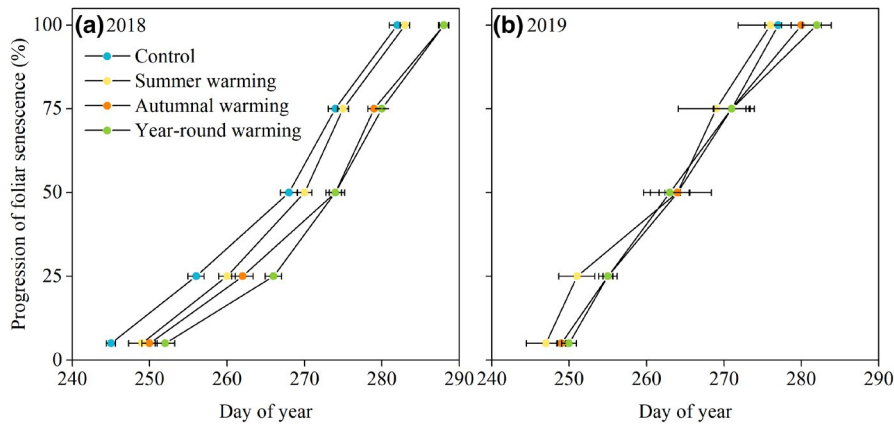


**FIGURE 3** Average timing of autumnal foliar senescence (50% coloration) in the seasonal-warming treatments in 2018 (a) and 2019 (b). Different letters indicate significant differences ( $p < 0.05$ ) among the warming treatments. \*Significant difference between 2018 and 2019. Values are means  $\pm$  standard errors ( $n = 6$ , except  $n = 3$  in the summer-warming treatment and  $n = 5$  in the autumnal-warming treatment in 2019 due to seedling mortality)

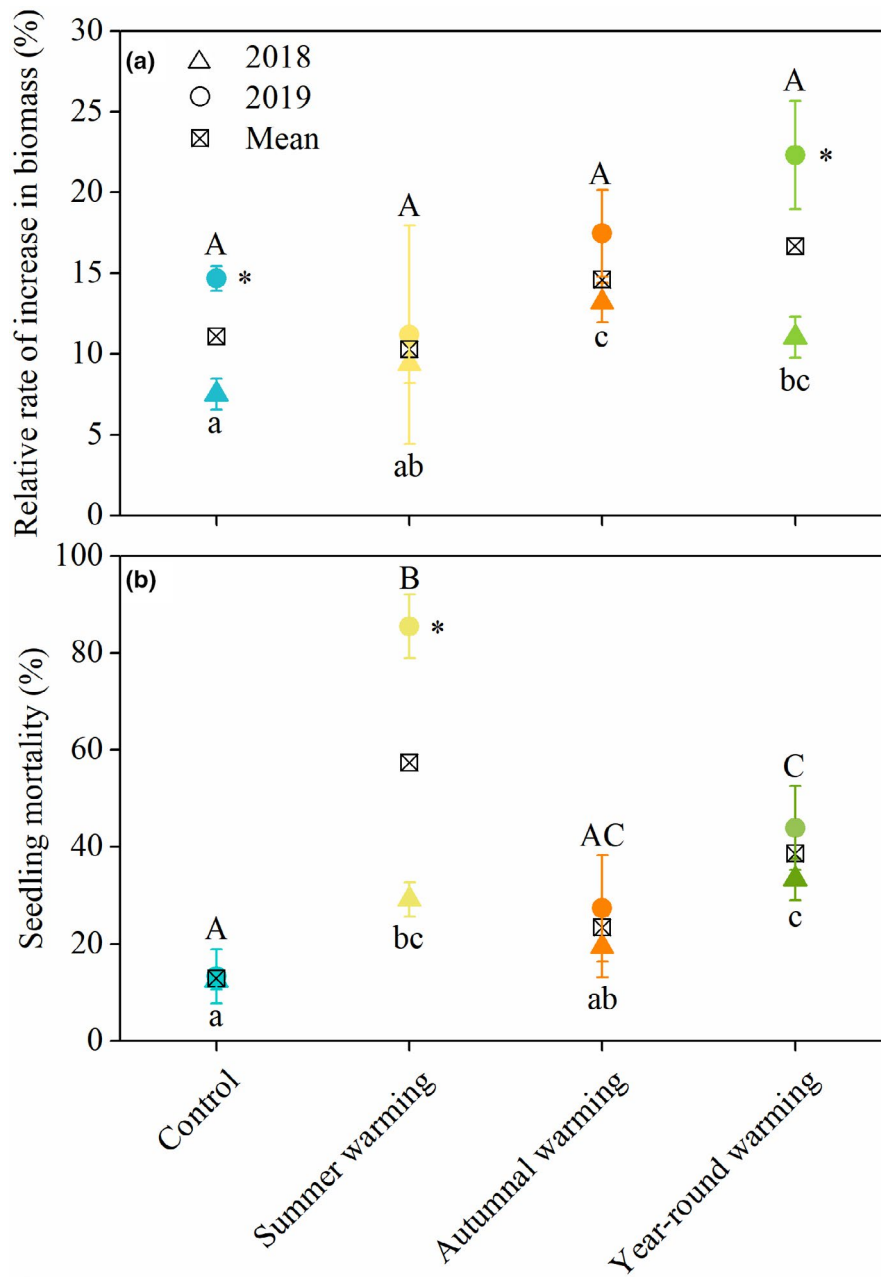
timing (50% coloration) of foliar senescence but delayed its onset (5% coloration; Table S1). Fu et al., (2018), however, observed a longer delay of foliar senescence with summer than autumnal warming for *Fagus sylvatica* L. saplings. This inconsistency may be because the lower temperatures in the autumn after the summer-warming treatment greatly accelerated senescence (Fracheboud et al., 2009; Fu et al., 2018). Interestingly, the timing of foliar senescence, however, did not differ significantly among the warming treatments in 2019. This is likely due to the extremely dry conditions in the summer and early autumn in 2019, which advanced foliar senescence probably due to carbon starvation and/or embolism by drought-induced stomatal closure, and thus offsetting the delaying effect of warming in

2018. We found that the air temperature was similar between 2018 and 2019 (summer/autumn period), but clear decrease and increase patterns were observed in soil-water content and VPD, respectively, in 2019 relative to 2018, especially in autumn. Besides, the relative changes induced by warming treatment in soil-water content and VPD were higher and lower, respectively, in 2019 relative to 2018. These results suggested that other environmental factors potentially involved with the foliar senescence processes, and the soil-water content and the VPD (driven by interannual precipitation variability and warming treatment) were likely co-determine the autumnal foliar senescence processes in 2019. These results highlight the importance of the availability of water in mediating the phenological





**FIGURE 4** Progression (i.e., 5, 25, 50, 75, and 100%) of foliar senescence in the seasonal-warming treatments in 2018 (a) and 2019 (b). Values are means  $\pm$  standard errors ( $n = 6$ , except  $n = 3$  in the summer-warming treatment and  $n = 5$  in the autumnal warming treatment in 2019 due to seedling mortality)



**FIGURE 5** Relative rates of increase in total biomass (a) and mortality (b) of the larch seedlings in the seasonal-warming treatments in 2018 and 2019, and the averages of the 2 years. Different lower- and uppercase letters indicate significant ( $p < 0.05$ ) differences among the warming treatments in 2018 and 2019, respectively. \*Significant difference between 2018 and 2019. Values are means  $\pm$  standard errors ( $n = 6$ , except  $n = 3$  in the summer-warming treatment and  $n = 5$  in the autumnal warming treatment in 2019 due to seedling mortality for the relative rates of increase in total biomass). We used basal diameter at the beginning of 2020 instead of at the end of 2019 for calculating biomass due to the unavailability of data

responses to seasonal warming. The notion that variations of foliar autumnal phenology are dominated by temperature, regardless of the hydrological conditions, is probably problematic and simplistic. Previous studies have reported the legacy effects between spring and autumnal phenophases (Fu et al., 2014; Yan et al., 2020; Zohner & Renner, 2019). However, most of these studies focused on the legacy effects of spring phenology on the following autumnal or spring phenophases, or the autumnal phenology on the following spring phenology, long-term experimental studies, especially autumn phenology in two consecutive years, to our knowledge, has not yet been reported. We did not find significant relationships in the timing of autumnal phenology between 2018 and 2019, but this does not mean an absent of the legacy effect, on the contrary we speculate that the legacy effects of autumnal phenology between 2018 and 2019 and other environmental and growth cues determined the autumnal phenology processes (Zani et al., 2020). However, due to the limitations of our study, further well-designed manipulative experiments are necessary to confirm our speculation, and also to investigate the potential differences between seedlings and mature trees.

The responses of foliar senescence to autumnal and year-round warming were associated with a similar sensitivity of foliar senescence to temperature of 6.7–8.3 d/°C (Figure S2), which is comparable to the values of 6–8 d/°C reported by Fu et al., (2018) and of 5.0–7.3 d/°C reported by Han et al., (2014). The lack of a detectable difference in the sensitivity of autumnal foliar senescence to temperature between the treatments with autumnal and year-round warming again confirmed that warmer autumns dominantly drive the delay of foliar senescence.

#### 4.2 | Higher growth rate under autumnal warming

Warmer temperatures and longer growing seasons generally improve tree growth (de Cárcer et al., 2018; Piao et al., 2007). Autumnal warming in the wet 2018 in our study significantly increased plant productivity (i.e., increased total biomass), whereas summer warming did not significantly affect productivity, indicating the divergent responses of tree growth to nonuniform seasonal warming, partly supporting our first hypothesis. The increased growth of seedlings under the autumnal-warming treatment may result from two possible causes. First, delayed foliar senescence increases photosynthetic carbon gains due to the later degradation of chlorophyll and extends the growing season (source-driven timing of foliar senescence; de Cárcer et al., 2018; Shi et al., 2015). Second, higher temperatures extend the growth of wood and lead to a later foliar senescence (sink-driven timing of foliar senescence; Dox et al., 2020). Our results suggest that the larch seedlings could gain a competitive advantage (e.g., more carbon assimilation, longer wood growth) under warmer and favorable hydrological conditions in autumn. Zohner et al., (2019) similarly found that delayed foliar senescence could substantially compensate (25–31%) shorter growing seasons induced by spring frost.

#### 4.3 | Seedling mortality under summer warming and other potential risks of warming

Higher temperatures can decrease the resilience of plants to drought, increasing plant mortality (Allen et al., 2010). Our manipulative experiment found that seedling mortality was significantly higher for both summer and year-round warming than for the control treatment, especially in the dry 2019 compared to the wet 2018. This finding is consistent with a study by Morin et al., (2010) reporting that warming induced higher mortality (by about 30%) in the seedlings of three species of European oaks and with a study by Neumann et al., (2017) demonstrating that a 2°C increase in Europe in the summer temperature of the preceding year increased tree mortality by 18% in the subsequent year. In addition to the impact of summer temperature, low precipitation may also have driven the mortality of seedlings. Precipitation in the summer (June, July, and August) of 2019 was extremely low (186 mm), only accounting for ~39% of the corresponding precipitation in 2018 and 64% of the long-term mean (from 1969 to 2019).

Larch seedlings will likely benefit from autumnal warming under future climatic warming, and a longer growing season could potentially increase total biomass by 0.49–0.93%/d, but the seedlings may also suffer from summer warming and drought, thereby increasing mortality. The potentially higher likelihood of the risk of autumnal frost damage is nonetheless another possible implication of the delay in foliar senescence (Liu et al., 2019), but whether and how the response differs (e.g., magnitude) between seedlings and older trees need to be verified. How the interaction between warming and drought determines growth and mortality, and the ontogenetic difference in the response of autumnal phenology also needs further study, especially on more tree species and different climatic zones.

### 5 | CONCLUSIONS

We provided experimental evidence that the timing of autumnal foliar senescence and growth respond differentially to nonuniform seasonal warming. Autumnal foliar senescence was delayed in the treatments with autumnal and year-round warming in the wet 2018 but not the dry 2019. Autumnal warming increased the rate of seedling growth, whereas summer warming caused higher seedling mortality. These results suggest that the availability of water substantially mediates the phenological and growth performances to warming. Our *in situ* experimental results provide new insights into the processes of foliar senescence that play a pivotal role in regulating the carbon cycle and hence the feedbacks to climate change (Fridley, 2012; Piao et al., 2008). The asymmetric responses of autumnal foliar senescence, productivity, and mortality to nonuniform seasonal warming should thus be incorporated into phenological models and/or the phenological modules in Earth system models to more accurately predict carbon, water, and energy balances in a warmer world.

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## DATA AVAILABILITY STATEMENT

All data are included in the article and the appendix containing supplementary information.

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## SUPPORTING INFORMATION

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

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