

## Physiological and growth responses to experimental warming in first-year seedlings of deciduous tree species

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Received: 27.11.2016 • Accepted/Published Online: 03.04.2017 • Final Version: 14.06.2017

**Abstract:** Increasing temperature might affect physiological and growth traits of seedlings, which are particularly important for tree survival. This study was conducted to investigate the physiological and growth responses of first-year seedlings to open-field experimental warming during one growing season. Seedlings of three deciduous tree species (*Fraxinus rhynchophylla* Hance, *Zelkova serrata* (Thunb.) Makino, and *Quercus variabilis* Blume) were warmed with infrared heaters with a mean air temperature difference of 3.07 °C between the treatments. Physiological traits (net photosynthetic rate, transpiration rate, stomatal conductance, and total chlorophyll content) were measured in July, September, and October 2014, and growth traits (root collar diameter (RCD), shoot length, component biomass, and root mass to stem mass ratio (RSR)) were measured in June, August, and October 2014 for harvested seedlings. Net photosynthetic rate, transpiration rate, and stomatal conductance were not affected by the warming treatment, whereas total chlorophyll content increased. Shoot length, leaf biomass, and stem biomass were enhanced under the warming treatment, whereas RCD and root biomass did not differ between the treatments. Thus, relative root growth declined under the warming treatment. It is likely that the elevated temperature provides optimal conditions for the biosynthesis of chlorophyll. Moreover, seedlings allocated more carbon to aboveground growth than to belowground growth when temperatures were elevated. In contrast, net photosynthetic rate, transpiration rate, and stomatal conductance were hindered, failing to increase as an adaptive mechanism to warming-induced water stress. Further studies are needed to elucidate (1) the direct effect of a decline in soil moisture, (2) why RSR declines to different extents in different species, and (3) the relationship between decreased root growth and seedling survival under the warming treatment.

**Key words:** Ash, experimental warming, Japanese Zelkova, oriental oak, seedling growth

### 1. Introduction

Global warming is expected to increase the surface temperature of the Earth by 1.1–2.6 °C by the end of the 21st century (2081–2100) relative to 1986–2005 (IPCC, 2014) with these elevated temperatures leading to water stress (Wan et al., 2007). Temperature is a key driver of the developmental processes of forest ecosystems, and the meta-analysis results of woody plants reported that the warming treatment either stimulates or suppresses the physiological and growth responses of seedlings (Wu et al., 2011). Such changes to the physiology and growth of plants under warming strongly influence their productivity, competitive ability, and long-term establishment (Arend et al., 2011; Lin et al., 2012).

In another study, the physiology and growth of trees could increase or decrease by warming (Chung et al., 2013), and the impacts of warming varied depending on where trees are distributed (Fisichelli et al., 2012). Moreover, the response of trees to elevated temperature differs with respect to species or provenance, rather than broader functional groups, such as biome or taxonomy (Saxe et al., 2001; Fisichelli et al., 2014). In particular, temperate broadleaf species, especially deciduous species, exhibited an enhanced growth response to warming (Carter, 1996; Way and Oren, 2010). Elevated temperatures cause an increase in the shoot height, stem diameter, stem volume, and stem mass, all of which are indicators of tree growth; however, the magnitude of response varied across species

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(Way and Oren, 2010). Elevated temperature also enhances the growth of temperate broadleaf seedlings; however, the degree and direction of responses by seedlings might differ to those of mature trees (Fisichelli et al., 2014).

The seedling stage appears to exhibit more sensitive stress responses than mature trees; thus, this stage is important for the successful establishment of trees (Danby and Hik, 2007). In particular, warming has a greater impact on the photosynthesis, biomass allocation, and growth of seedlings compared to mature trees, because seedlings have shallower root systems (Niinemets, 2010; Khaine and Woo, 2015). Consequently, because changes to temperature, soil water content, light, and nutrients by warming affect the physiology of trees, these factors influence the survival rate and future growth rates of seedlings after planting (Sung et al., 2011). Han et al. (2015) suggested that seedling growth exhibits a species-specific response to altered net photosynthetic rate, chlorophyll content, and leaf area. Therefore, studies on how seedlings of different species respond to the warming treatment are required. Moreover, the growth responses during the seedling stage are particularly important for the management of forestry, since 1-year-old seedlings of deciduous species are widely used for planting in Korea (Korea Forest Service, 2012).

The current study aimed to investigate the physiological and growth responses of seedlings from three deciduous species (*Fraxinus rhynchophylla* Hance, *Zelkova serrata* (Thunb.) Makino, and *Quercus variabilis* Blume) to open-field experimental warming using infrared heaters. Specifically, this study aimed to: (1) characterize how warming treatment affects the physiological (net photosynthetic rate, transpiration rate, stomatal conductance, and total chlorophyll content) and growth (root collar diameter (RCD), shoot length, component biomass, and root mass to stem mass ratio (RSR)) traits of first-year seedlings, and (2) determine whether the treatment effect differs with the species.

## 2. Materials and Methods

### 2.1. Experimental design

An experimental warming system was built in the Forest Practice Research Center, National Institute of Forest Science, Pocheon, Gyeonggi-do, Korea (37°45'N, 127°10'E) in October 2011 (Han et al., 2015). *F. rhynchophylla*, *Z. serrata*, and *Q. variabilis* seeds were sown separately in the control and warmed plots (1 m × 1 m each, 6 plots per species, 18 plots total with n = 3) on 24 April 2014. Initial seeding density (seeds m<sup>-2</sup>) was as follows: *F. rhynchophylla*, 887 seeds m<sup>-2</sup>; *Z. serrata*, 1758 seeds m<sup>-2</sup>; and *Q. variabilis*, 315 seeds m<sup>-2</sup>. The seedlings were thinned following germination on 2 July 2014. The resulting densities were in accordance with those proposed

by the Korea Forest Service (2012) silviculture guidelines: *F. rhynchophylla*, 90 seedlings m<sup>-2</sup>; *Z. serrata*, 81 seedlings m<sup>-2</sup>; and *Q. variabilis*, 90 seedlings m<sup>-2</sup>.

*F. rhynchophylla* is a common, naturally regenerating hardwood species (Yeo and Lee, 2006) that is distributed throughout Korea. *Z. serrata* is a broad-leaved deciduous tree species that is found in China and Japan (Fukatsu et al., 2005). *Quercus* spp. are globally distributed, occupying a wide range of habitats in temperate regions (Arend et al., 2011). *Quercus* spp. dominate most wooded habitats in temperate regions, accounting for approximately 26% of the total forested area in Korea (Lee et al., 2004).

Infrared heaters (FTE-1000, Mor Electric Heating Assoc. Inc., Comstock Park, MI, USA) were used for the heating module, whereas dummy heaters were installed in the control plots to simulate the shading effects of the heaters. The distance between the infrared heaters and the tops of seedlings was approximately 80 cm. The warming system has been operated since October 2012, and the newly germinated seedlings in the warmed plots were warmed to maintain the air temperature 3 °C higher than that of the control plots. Infrared temperature sensors (SI-111, Campbell Scientific, Inc., Logan, UT, USA) and data loggers (CR-1000, Campbell Scientific, Inc.) were used to monitor the air temperature differences between the treatments. Relays controlled the system based on the simultaneous measurement of the temperatures between the treatments. Soil temperature and moisture content were monitored using a sensor (5TM, Decagon, Pullman, WA, USA). Annual mean air temperatures were 3.07 °C higher and mean soil temperature was 2.06 °C higher under the warming treatment in 2014. The annual mean soil moisture content was lower in the warmed plots compared to the control plots (control: 8.18%, warmed: 6.13%, n = 3).

### 2.2. Measurements of physiological and growth responses

The net photosynthetic rate, transpiration rate, and stomatal conductance of seedlings were measured for 3–4 days starting on 29 July, 26 September, and 24 October 2014 depending on the weather conditions, between 0900 and 1200 hours using a portable photosynthesis system (CIRAS-2, PP-Systems, Amesbury, MA, USA) and a leaf chamber (PCL 6 (U) Automatic Universal Leaf Cuvette, PP-Systems). The conditions during the measurement were as follows: photosynthetic photon flux density was maintained at 1000–1100 μmol m<sup>-2</sup> s<sup>-1</sup> with an LED lamp and the reference CO<sub>2</sub> concentration was 400 ± 2 ppm. In each plot, two seedlings were randomly selected, and the net photosynthetic rate, transpiration rate, and stomatal conductance for a leaf from each seedling were measured with three replicates. After the measurements, the leaves were sampled to measure total chlorophyll content. A quantity of 20 ± 3 mg leaves was cut into 2-mm pieces

and incubated in 5 mL of dimethyl sulfoxide (DMSO) at 65 °C for 60 min in a boiling water bath in the dark. The absorbance of chlorophyll extracts was measured using a spectrophotometer (U-1100, Hitachi, Tokyo, Japan) at 648 nm and 665 nm, and total chlorophyll content was calculated (Barnes et al., 1992).

Five seedlings per plot representative of the average growth were harvested on 19 June, 27 August, and 30 October 2014. The RCD and shoot length of the seedlings were measured using digital calipers (3418 Traceable Digital Calipers, Control Company, Webster, TX, USA) and rulers, respectively. Leaves, stems, and roots were separated, dried, and weighed. For leaves, total leaf area of seedlings was measured in August 2014 using WinSEEDLE V4.4A (Regent Instruments Inc., Quebec, QC, Canada). Based on the component measurements, RSR was calculated for each seedling.

### 2.3. Statistical analysis

All statistical analyses were performed using SAS 9.4 statistical software (SAS Institute, Cary, NC, USA). Repeated-measures ANOVA was used to assess differences in the net photosynthetic rate, transpiration rate, stomatal conductance, total chlorophyll content, RCD, shoot length, component biomass, and RSR between the control and warmed plots, and the interaction among the effects of the warming treatment, measurement time, and species ( $P < 0.05$ ). If the warming treatment was reported to have a significant effect, the means of the individual treatments within each species group were compared using the LSD test ( $P < 0.05$ ).

### 3. Results

There was no significant effect on net photosynthetic rate, transpiration rate, or stomatal conductance with the warming treatment, and no interactions between the treatments and species or month (Table 1). There was no certain tendency in differences between the treatments for each of the values (Table 2).

The warming treatment had a significant effect on total chlorophyll content (Table 1). Total chlorophyll content tended to increase under the warming treatment, while it was only statistically significant for *Q. variabilis* in July and September (Table 3). Nevertheless, there was no significant interaction between the treatments and the species (Table 1).

The warming treatment had a significant effect on shoot length, leaf biomass, and stem biomass with a significant interaction between the treatments and month (Table 1). The warming treatment did not affect RCD or root biomass, and the interactions between the treatments and species or month were not significant (Table 1). Shoot length, leaf biomass, and stem biomass were consistently higher under the warming treatment, whereas there was minimal significance in each species and month (Figures 1 and 2). Shoot length increased in August and October for *Z. serrata* and increased in August for *Q. variabilis*. Leaf biomass increased in August for *Q. variabilis* under the warming treatment. Stem biomass increased in August and October for *Z. serrata*, and increased in August for *Q. variabilis*.

RSR decreased with the warming treatment, and there was a significant interaction between the treatments

**Table 1.** Results of the repeated measures ANOVA for variables.

Variable	F-value						
	Sp	Trt	Sp × Trt	Month	Sp × Month	Trt × Month	Sp × Trt × Month
$P_n$	1.29	0.53	1.38	1.9	1.7	1.57	1.59
E	0.70	0.39	0.80	0.00	2.56	2.21	0.35
$g_s$	0.82	1.40	0.89	8.91***	2.88*	2.41	0.35
Total chl	22.83***	8.6*	2.16	55.35***	23.19***	0.64	0.51
RCD	1.56	0.38	0.75	176.56***	4.47*	0.66	0.58
Shoot length	119.43***	15.1**	2.13	235.59***	52.43***	4.19*	0.95
Leaf biomass	12.71**	9.37*	0.76	60.39***	4*	4.5*	1.54
Stem biomass	13.91**	14.6**	2.23	130.96***	8.82**	5.87*	1.02
Root biomass	37.16***	1.46	0.35	107.52***	26***	0.53	0.14
RSR	297.23***	21.7**	9.46**	56.11***	61.26***	3.81*	2.82

×: interaction effect, Sp: species, Trt: treatment,  $P_n$ : net photosynthetic rate, E: transpiration rate,  $g_s$ : stomatal conductance, Total chl: total chlorophyll content, RCD: root collar diameter, RSR: root mass to stem mass ratio  
\*, \*\*, and \*\*\* mean  $P < 0.05$ ,  $P < 0.01$ , and  $P < 0.001$ , respectively.

**Table 2.** Net photosynthetic rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), transpiration rate ( $\text{mmol m}^{-2} \text{ s}^{-1}$ ), and stomatal conductance ( $\text{mmol m}^{-2} \text{ s}^{-1}$ ) of first-year seedlings of *Fraxinus rhynchophylla*, *Zelkova serrata*, and *Quercus variabilis* in the control and warmed plots in July, September, and October. The numbers represent the mean with standard error in parentheses.

Species	Treatment	$P_n$			E			$g_s$		
		Jul.	Sep.	Oct.	Jul.	Sep.	Oct.	Jul.	Sep.	Oct.
<i>F. rhynchophylla</i>	Control	12.80 (1.31)	9.58 (0.71)	3.49 (1.21)	3.73 (0.28)	4.11 (0.60)	3.05 (0.18)	201.39 (23.74)	462.63 (109.03)	190.61 (24.88)
	Warmed	13.57 (2.67)	10.32 (1.99)	15.36 (7.78)	4.43 (0.92)	4.42 (0.42)	2.78 (0.92)	281.91 (80.65)	472.52 (34.03)	164.18 (57.35)
<i>Z. serrata</i>	Control	11.73 (0.75)	8.14 (0.40)	8.30 (1.66)	3.71 (0.13)	3.93 (0.81)	4.64 (0.38)	208.03 (17.44)	394.15 (118.67)	357.29 (48.24)
	Warmed	14.00 (0.10)	5.53 (1.39)	12.88 (4.94)	4.63 (0.51)	3.31 (0.65)	3.96 (0.80)	257.99 (44.37)	260.54 (65.96)	277.67 (88.86)
<i>Q. variabilis</i>	Control	11.10 (0.46)	15.07 (2.04)	13.73 (3.31)	3.49 (0.40)	5.10 (0.48)	4.79 (0.42)	179.29 (32.26)	590.21 (143.75)	403.57 (19.49)
	Warmed	11.67 (0.71)	11.83 (3.01)	12.16 (0.55)	3.95 (1.03)	3.56 (0.73)	4.02 (0.66)	222.83 (63.99)	360.58 (126.99)	303.07 (72.56)

$P_n$ : net photosynthetic rate, E: transpiration rate,  $g_s$ : stomatal conductance

**Table 3.** Total chlorophyll content ( $\text{mg g}^{-1}$ ) of first-year seedlings of *Fraxinus rhynchophylla*, *Zelkova serrata*, and *Quercus variabilis* in the control and warmed plots in July, September, and October. Bold values indicate statistical significance between the treatments ( $P < 0.05$ ,  $n = 3$ ). The numbers represent the mean with standard error in parentheses.

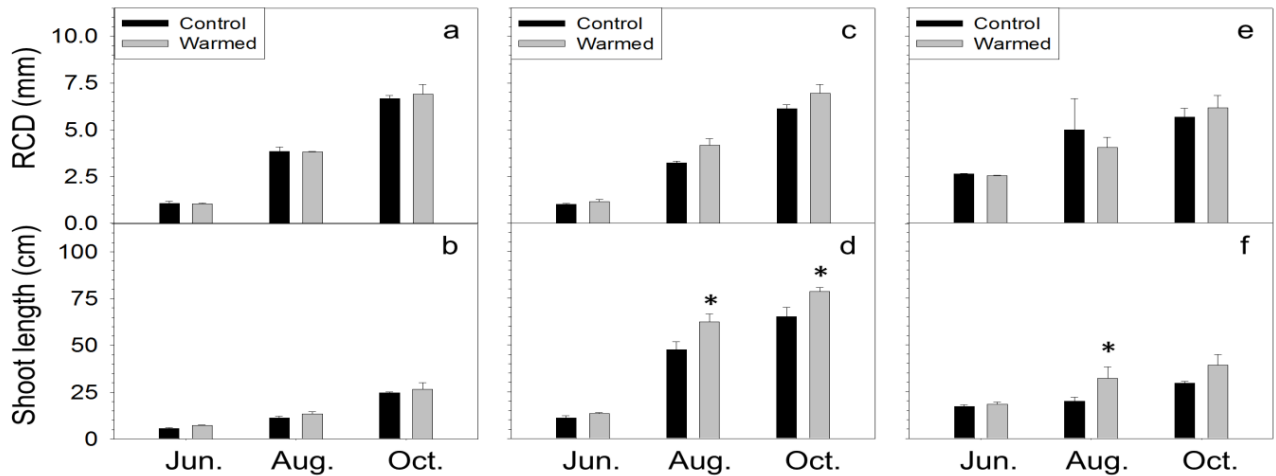
Species	Treatment	Total chlorophyll content		
		Jul.	Sep.	Oct.
<i>F. rhynchophylla</i>	Control	1.72 (0.17)	2.40 (0.14)	1.58 (0.21)
	Warmed	2.27 (0.29)	2.47 (0.19)	1.64 (0.47)
<i>Z. serrata</i>	Control	2.41 (0.12)	2.11 (0.25)	1.99 (0.30)
	Warmed	2.56 (0.25)	2.19 (0.25)	2.16 (0.14)
<i>Q. variabilis</i>	Control	<b>3.23 (0.12)</b>	<b>3.51 (0.18)</b>	1.15 (0.07)
	Warmed	<b>4.02 (0.17)</b>	<b>4.45 (0.31)</b>	1.60 (0.06)

and the species or month (Table 1). In detail, the RSR of *Q. variabilis* significantly decreased with the warming treatment in August and October. Total leaf area tended to increase under the warming treatment, and the difference between the treatments was statistically significant for *Z. serrata* in August (Table 4).

#### 4. Discussion

##### 4.1. Physiological and growth responses to the warming treatment

This study showed that the warming treatment caused total chlorophyll content to increase with no difference in warming effect depending on the species or month.



**Figure 1.** Root collar diameter (RCD) and shoot length of first-year seedlings of *Fraxinus rhynchophylla* (a, b), *Zelkova serrata* (c, d), and *Quercus variabilis* (e, f) in the control and warmed plots in June, August, and October. Error bars denote standard error of mean. The asterisks indicate statistical significance between the treatments ( $P < 0.05$ ,  $n = 3$ ).

In general, chlorophyll content increases with rising air temperature (Saxe et al., 2001). A previous study showed that warming treatment using infrared heaters greatly increased total chlorophyll content; thus, the elevated temperature might provide near-optimal conditions for chlorophyll biosynthesis (Zhao and Liu, 2009).

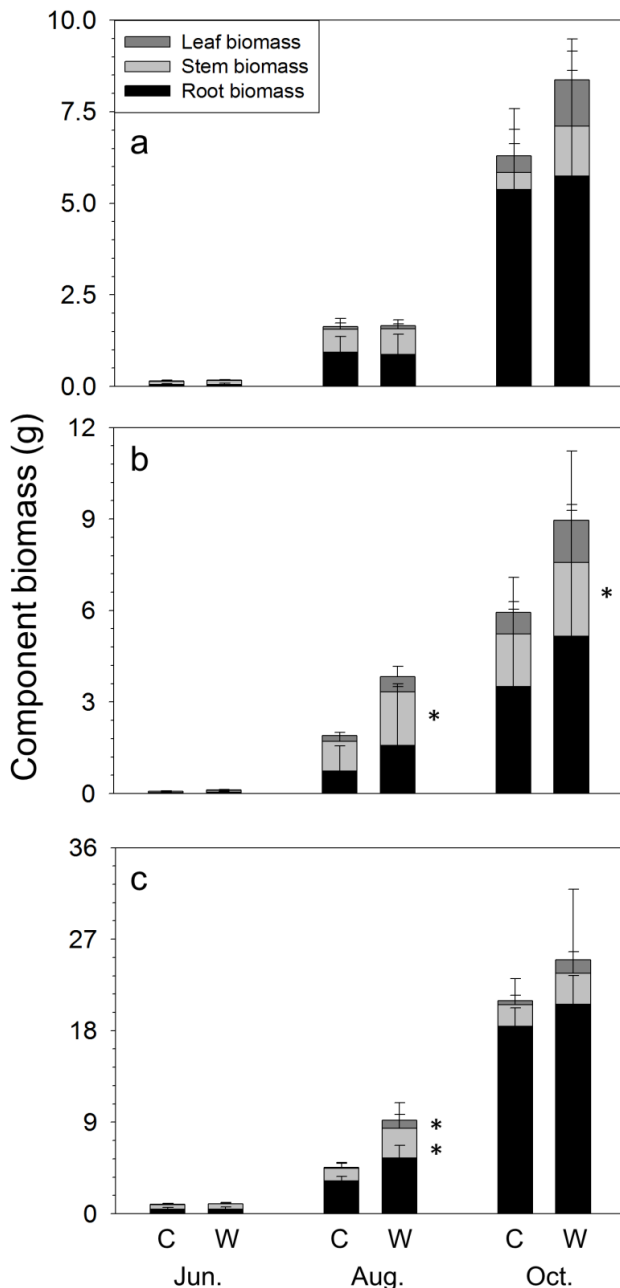
The photosynthetic rate is influenced by the elevated temperature through changes in physiological traits, such as photosynthetic pigment content (Saxe et al., 2001). Changes in chlorophyll content affect the net photosynthetic rate of *Picea asperata* and *Abies faxoniana* (Yin et al., 2008). However, despite an increase in total chlorophyll content, there was no significant change in net photosynthetic rate with the warming treatment in this study.

The results of the current study showed no significant change in transpiration rate or stomatal conductance. Unchanged stomatal conductance with an elevated temperature could indicate that gas exchange through stomata is not affected. Controlled stomatal conductance might be an adaptation mechanism to prevent the transpiration rate and net photosynthetic rate from increasing (Farquhar and Sharkey, 1982). Seedlings might use this adaptation to cope with water stress under warming treatment, since soil moisture content is reduced by the warming treatment with water stress increasing if the transpiration rate and net photosynthetic rate increase (Seneviratne et al., 2010; Zhu et al., 2017).

Our results showed that the warming treatment caused seedling growth to significantly increase, even though the net photosynthetic rate was not changed. Way and Oren (2010) suggested that deciduous trees exhibit higher growth rates under warming conditions, which might lead

to more biomass being allocated to leaves. However, the net photosynthetic rate is not always proportional to growth responses (Saxe et al., 2001). Seedling growth might be enhanced by an increase in the total leaf area of plants in the warming treatment, regardless of unchanged net photosynthetic rates, even though the specific mechanism is not clear. That is, the measured net photosynthetic rate per unit leaf area was similar between the treatments. Nevertheless, the net photosynthetic rate of the seedling as a whole might have increased because the total possible photosynthetic leaf area was enhanced following exposure to the warming treatment. Therefore, carbon allocation might be more important than photosynthesis as an acclimation mechanism to environmental change (Domisch et al., 2002). Atkin and Tjoelker (2003) defined thermal acclimation as an adjustment of the metabolic rate that compensates for a change in growth temperature, potentially resulting in metabolic homeostasis.

By comparing the results of RCD and root biomass with shoot length and aboveground biomass including leaf and stem biomass, the warming treatment appeared to affect aboveground growth more than belowground growth. Fisichelli et al. (2014) reported that stem length increased in first-year temperate broadleaf seedlings when temperatures were 3 °C higher than the ambient. The review by Way and Oren (2010) suggested that the root to shoot ratio declines with increasing temperature, due to an increase in leaf and stem mass and a nonsignificant change in root mass for broad-leaved deciduous trees. Moreover, seedlings allocate more biomass to aboveground growth and less to belowground growth in response to the elevated temperatures (Way and Oren, 2010).



**Figure 2.** Component biomass of first-year seedlings of *Fraxinus rhynchophylla* (a), *Zelkova serrata* (b), and *Quercus variabilis* (c) in the control and warmed plots (C: control, W: warmed). The asterisks indicate a significant increase in each component biomass compared to the control, and error bars denote standard error of mean ( $P < 0.05$ ,  $n = 3$ ).

Lack of change in root growth accompanying enhanced aboveground growth may cause the decrease in RSR. It can be construed as a coping mechanism of seedlings that were already adapted to water stress by controlling stomatal activity. The decreased proportion of root growth

could confer an adaptive advantage by concentrating the resource investment in assimilating organs when soil moisture is not a limiting factor (Yin et al., 2008).

In addition, the effect of the warming treatment on RSR differed with the species. This might have resulted from the fact that the biomass allocation to roots varied with the species; nevertheless, the detailed reason or mechanism is not clear. In this study, the decreasing rate of RSR was faster when the original relative root mass was large. Therefore, further studies should be conducted to elucidate accurate mechanisms behind the different decreasing rate of RSR depending on the species observed in the current study.

#### 4.2. Management implications

The current study showed that the warming treatment caused the aboveground growth and total leaf area to increase, whereas the relative root growth declined. Root mass is a useful indicator for assessing the potential performance of seedlings with lower relative root growth potentially reducing the survival rate of seedlings early after transplantation (Budiman et al., 2015). In particular, 1-year-old and 2-year-old seedlings are widely used for plantations in Korea; however, how seedling survival is affected by a decline in root growth due to the elevated temperature needs clarification. The initial growth rates at the early developmental stage might influence their quality, such as shoot weight, root weight, total seedling weight, RCD, and seedling height (Dickson et al., 1960). Therefore, our results on how warming affects the survival of early-stage seedlings could be used to revise the management strategies of silviculture. Such changes could enhance the success of transplantation and even lead to the production of higher quality seedlings (Skinner, 2007).

#### 4.3. Conclusions

Our results showed that the warming treatment had a significant impact on total chlorophyll content, aboveground growth, and relative root proportion. The warming treatment affected physiological traits, in terms of adaptation to water stress, which was accompanied by selective carbon allocation to aboveground growth; however, we only investigated the impact of decreased soil moisture accompanied by elevated temperature in the current study. Therefore, multifactorial experiments that can evaluate the direct effect of a decline in soil moisture would be helpful for examining the influences of a wide range of possible climate change scenarios. In addition, our results provide important information to forest managers on how trees cope with rising temperatures and could be used to adjust management practices. Future studies should investigate the correlation between the decline in relative root growth and seedling survival for each species to supplement existing management strategies of

**Table 4.** Root mass to stem mass ratio (RSR) and total leaf area (cm<sup>2</sup> seedling<sup>-1</sup>) of first-year seedlings of *Fraxinus rhynchophylla*, *Zelkova serrata*, and *Quercus variabilis* in the control and warmed plots in June, August, and October and in August, respectively. The numbers represent the mean with standard error in parentheses (n = 3).

Species	Treatment	RSR			Total leaf area
		Jun.	Aug.	Oct.	Aug.
<i>F. rhynchophylla</i>	Control	2.36 (0.28)	2.25 (0.12)	2.59 (0.20)	97.39 (18.78)
	Warmed	1.74 (0.16)	1.72 (0.09)	2.01 (0.15)	112.29 (17.41)
<i>Z. serrata</i>	Control	1.38 (0.25)	0.93 (0.05)	1.19 (0.19)	166.45 (17.85)
	Warmed	1.52 (0.07)	0.88 (0.10)	0.90 (0.05)	275.57 (26.54)
<i>Q. variabilis</i>	Control	2.70 (0.17)	8.07 (0.27)	11.71 (0.89)	196.84 (25.58)
	Warmed	2.50 (0.35)	5.74 (1.14)	8.17 (0.45)	452.77 (87.90)

silviculture. Moreover, silvicultural guidelines should be revised to incorporate the impact of climate change, since the growth of first-year seedlings influences survival rates and future growth dynamics.

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