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Effects of experimental warming on soil respiration and biomass in *Quercus variabilis* Blume and *Pinus densiflora* Sieb. et Zucc. seedlings

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Abstract
· *Key message* In the open-field warming experiment using infrared heaters, 3 °C warming affected soil respiration more in the deciduous *Quercus variabilis* Blume plot than in the evergreen *Pinus densiflora* Sieb. et Zucc. plot, but did not affect the plant biomass in either species.
· *Context* Understanding the species-specific responses of belowground carbon processes to warming is essential for the accurate prediction of forest carbon cycles in ecosystems affected by future climate change.

· *Aims* This study aimed to investigate the effect of experimental warming on soil CO_2 efflux, soil-air CO_2 concentration, and plant biomass for two taxonomically different temperate tree species.
· *Methods* Experimental warming was conducted in an open-field planted with *Q. variabilis* and *P. densiflora* seedlings. Infrared heaters increased the air temperature by 3 °C in the warmed plots compared with the air temperature in the control plots over a 2-year period.
· *Results* The increase in air and soil temperature stimulated soil CO_2 efflux by 29 and 22 % for the *Q. variabilis* and *P. densiflora* plots, respectively. Seasonal variation in the warming effect on soil CO_2 efflux was species-specific. Soil CO_2 efflux was also positively related to both soil temperature and soil water content. The soil moisture deficit decreased the difference in soil CO_2 efflux between the control and warmed plots. Warming did not affect soil CO_2 concentration and plant biomass in either species; however, the mean soil CO_2 con-

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centration was positively correlated with root and total biomass.

• *Conclusion* Warming increased soil CO_2 efflux in both *Q. variabilis* and *P. densiflora* plots, while the increase showed remarkable seasonal variations and different magnitudes for the two species.

1 Introduction

Ongoing climate warming is expected to have a considerable impact on terrestrial carbon (C) dynamics by altering ecosystem functions and processes (IPCC 2013; Khaine and Woo 2015; Lu et al. 2013; Spittlehouse and Stewart 2003). To understand possible changes in the eco-physiological traits and biogeochemical properties of forest ecosystems, a growing number of warming manipulation studies have been conducted using tree seedlings (Chung et al. 2013; Fisichelli et al. 2014). Previous warming studies have suggested that elevated temperatures stimulate tree growth and photosynthesis, and extend the growing season of coniferous (Xu et al. 2012; Yin et al. 2008) and deciduous tree seedlings (e.g., Danyagri and Dang 2014; Kaye and Wagner 2014; Morin et al. 2010). However, the magnitude of these warming effects may differ according to plant functional group and biome (Lin et al. 2010; Way and Oren 2010). Fisichelli et al. (2014) recently reported the species-specific responses (e.g., emergence, leaf-out rate, and growth) of 15 North American tree species to climate change, identifying marked differences between the broadleaf temperate and coniferous groups.

Variation in the response of belowground components (e.g., soil and root respiration, root exudates, and microbial processes) to experimental warming can provide key information on the carbon transition from leaf photosynthesis to soil during rises in temperature (Atkin et al. 2000; Bradford et al. 2008; Liu et al. 2011; Yin et al. 2013). For example, a few recent studies have reported warming-induced soil respiration in silver birch, Norway spruce, and Scots pine seedlings growing in similar boreal ecosystems (Pumpanen et al. 2012), and in a dragon spruce plantation and natural forests (Xu et al. 2012; Yin et al. 2013). Soil respiration (R_S, soil CO_2 efflux) is an important natural source of CO_2 atmospheric emissions, as well as a representative indicator of soil biological activity (Schlesinger and Andrews 2000). Soil-air CO_2 concentration (SCO_2) determines the amount of CO_2 available for efflux from the soil to the atmosphere (Maier and Schack-Kirchner 2014). Because R_S and rhizosphere SCO_2 strongly depend on the photosynthetic activity of plants supplying carbohydrates from leaves to the roots and rhizosphere (Kuzyakov and Gavrichkova 2010), variation in forest canopy processes (e.g., leaf phenology, plant growth and

photosynthesis rates) is likely to influence belowground C dynamics (Inoue et al. 2012; Moyano et al. 2008). Therefore, the synthetic analysis of the responses of these parameters to warming can provide useful field evidence of the relationship between aboveground and belowground C processes (Flanagan et al. 2013; Li et al. 2011). In addition, detailed information about temporal variation in the effect of warming on R_S may aid in the understanding of responses among species with different leaf phenology (Contosta et al. 2011). However, few studies have investigated the seasonal impact of climate warming on R_S in two taxonomically different tree species.

The potential impact of climate change on the distribution of broad-leaved and coniferous tree species in the boreal zone were analyzed using observation and modeling in Northern Europe (Sykes and Prentice 1996) and British Columbia (Hamann and Wang 2006). *Pinus densiflora* Zieb. et Zucc. and *Quercus* species, which together occupy about 50 % of forest area in South Korea, are representative temperate coniferous and broad-leaved trees species, respectively (Korea Forest Service 2014). Based on future climate projections, tree growth models have predicted that *P. densiflora* forests in South Korea will gradually be replaced by *Quercus* forests (Byun et al. 2013; Kwak et al. 2012). However, the prediction should be validated with field evidence from artificial manipulation experiments (Rustad 2008). Our previous studies have demonstrated that artificial warming increases photosynthetic rates and the growing periods of *Quercus variabilis* Blume seedlings (Han et al. 2014a; Jo et al. 2011; Lee et al. 2012), while warming increases the leaf biomass and nitrogen content of *P. densiflora* seedlings (Lee et al. 2013). However, the species-specific responses of belowground C processes to warming remain unclear.
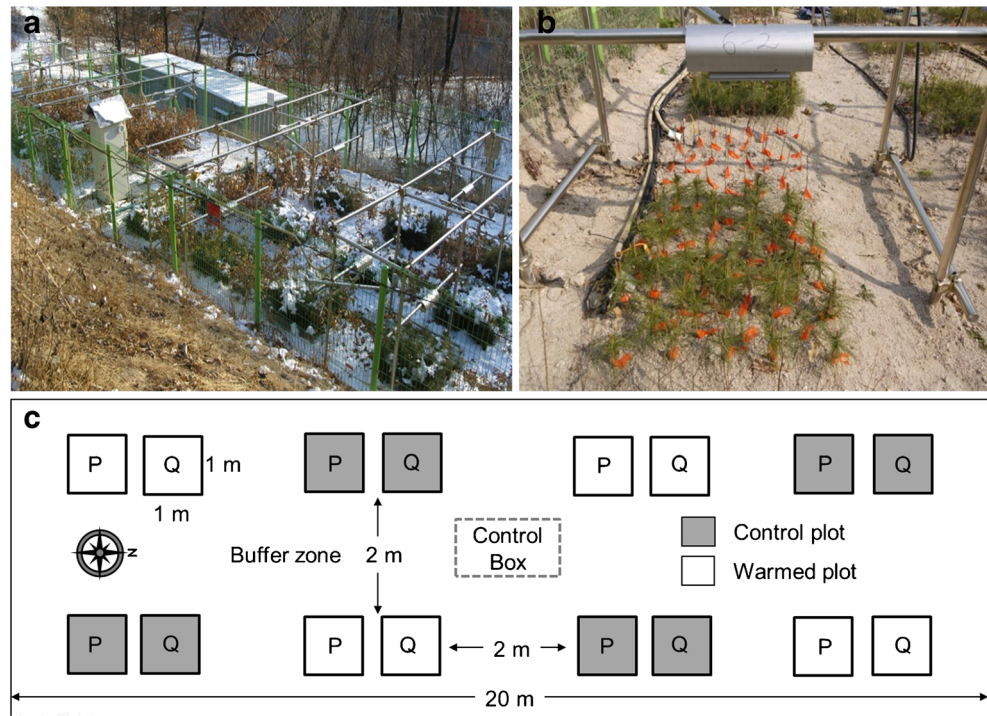
In this study, we examined the effects of warming on R_S, SCO_2, and plant biomass for seedlings of the deciduous *Q. variabilis* and the evergreen *P. densiflora* trees using infrared heaters. The study aimed to address the following questions: (1) How do R_S, SCO_2, and plant biomass for *Q. variabilis* and *P. densiflora* respond to warming? and (2) Is there seasonal variation in the magnitude of the warming effects? Generally, deciduous tree species are more sensitive to elevated temperatures than are evergreen trees (Way and Oren 2010). Therefore, we hypothesized that the R_S and SCO_2 responses in *Q. variabilis* seedlings to a rise in temperature would be more pronounced than in *P. densiflora* seedlings. These results will be useful for predicting species composition and C cycling in the face of future climate warming.

2 Materials and methods

2.1 Experimental design

This study was conducted at an experimental tree nursery (Fig. 1a) located in the Korea University Arboretum, Seoul,

Korea (37°35′36″N, 127°1′31″E). The annual mean air temperature and precipitation of the area are 12.5 °C and 1450.5 mm, respectively (1981–2010) (Korea Meteorological Administration 2015). In April 2010, a total of 16 experimental plots (1 × 1 m with a 2-m buffer between the plots) were established for the *Q. variabilis* Blume and *P. densiflora* Sieb. et Zucc. seedlings (Fig. 1c).

Soil and seedbed conditions were based on the open-field conditions at Korea University Arboretum. The mineral soil was collected from the forest close to campus of Korea University where the bedrock is characterized by granitic parent rock materials. After collection, the soil was sieved to remove coarse rocks. The soil is classified into sandy soil with a pH of 6.85 and a cation exchange capacity of 5.12 cmol kg^{-1}. Total C and N concentrations were 2.18 and 0.16 mg kg^{-1}, respectively (Jo et al. 2011). The tree species were *Q. variabilis* (Oriental oak), a deciduous broad-leaved tree, and *P. densiflora* (Japanese red pine), a coniferous tree. In May 2010, sixty-four 1-year-old *Q. variabilis* and ninety 1-year-old *P. densiflora* seedlings of similar sizes (i.e., of similar heights and root collar diameters) were planted in each plot (Lee et al. 2009). Subsequent thinning in March 2011 resulted in 35 *Q. variabilis* seedlings and 45 *P. densiflora* seedlings per plot (Fig. 1b). Open-field warming systems were set up in November 2010, consisting of eight infrared heaters (FTE-1000; Mor Electric Heating Instrument Inc., USA) in the warmed plots and eight dummy heaters of the same size and shape in the eight control plots. Each treatment (i.e., the control and warmed treatments for *Q. variabilis* [CQ and WQ] and the control and warmed treatments for *P. densiflora* [CP

and WP]) had four replications. The heaters were deployed at a height of about 60 cm above the seedling canopy at the center of each plot as it had been done in the study of Kimball et al. (2008). The warming system was designed to automatically maintain air temperature 3 °C warmer than the control plots by using the infrared heaters. The temperature differential was chosen according to IPCC SRES climate change scenario model predictions for the projected 3.26 °C increase in air temperature in South Korea by the year 2061 to 2070 compared to the mean value between 2001 and 2010 (KMA 2012). The differences in air temperature between the control and warmed plots for *Q. variabilis* were monitored using one infrared temperature sensors per plot (SI-111, Campbell Inc., USA) ($n = 4$). We assumed that, after accounting for the heat diffusion of air in an open-field system, for each *Q. variabilis* and *P. densiflora* plot pair, the air temperatures were homogeneous due to the equal distances between the seedling canopy surface and the infrared heater. The soil temperature at a depth of 5 cm and the volumetric soil moisture content at depths from 0 to 10 cm were measured in the center of each experimental plot using soil temperature sensors (108-LC, Campbell Inc., USA) and soil moisture sensors (CS616, Campbell Inc., USA) ($n = 16$), respectively. All data were recorded using data loggers (CR-3000, Campbell Inc., USA).

2.2 Measurements of soil CO_2 efflux and concentration

Soil CO_2 efflux (R_S) was measured using a closed chamber system with a portable diffusion-type non-dispersive infrared

(NDIR) CO_2 sensor (GMP343, Vaisala CARBOCAP, Finland), which has high selectively and sensitivity in open-air conditions (Yasuda et al. 2012), and a small chamber made of polyacrylics. The sensors were well calibrated at least once a year with standard CO_2 gases. The size of the chamber (10 cm in diameter, 12 cm in height) was designed so that it could be placed among high-density seedlings and allow the repetitive testing of linear changes in CO_2 inside the chamber. The chamber size was sufficiently small that it did not require an internal fan to ensure the mixing of gases. The sharp-edged chamber was directly inserted into the soil using clearly marked 2 cm-deep slits. A handheld control and logger (MI-70, Vaisala CARBOCAP, Finland) coupled with the NDIR CO_2 sensor recorded the CO_2 concentration every 5 s during a 300-s measurement period (Bekku et al. 1995). The first 30 s of data after the placement of the chamber were excluded from the subsequent analysis to allow for the initial adjustment of CO_2. R_S was calculated from the following formula

$$R_S = \frac{dCO_2}{dt} \times \frac{PV}{ART}$$

where P is the atmospheric pressure, V is the volume of the headspace gas within the chamber, A is the soil surface area enclosed by the chamber, R is the gas constant, and T is the air temperature (K) (Davidson et al. 1998). R_S measurements ($n=4$) were made between 10:00 and 14:00 monthly from June 2011 to April 2012.

Rhizosphere soil-air CO_2 concentration (SCO_2, μmol mol^{-1}) was monitored continuously at 1-h intervals using 16 NDIR CO_2 sensors (GMT222, Vaisala CARBOCAP, Finland) with a CR-3000 data logger from 2011 to 2012. One solid-state CO_2 sensor per plot was inserted vertically into centrally located holes pre-drilled to a 5-cm soil depth by an auger. An occasional malfunction of the data logging system in the summer resulted in some missing SCO_2 data. The missing data was 36 % in 2011 and 19 % in 2012.

2.3 Plant biomass

To measure the root and shoot biomass of the *Q. variabilis* and *P. densiflora* seedlings, the seedlings were excavated by carefully pulling them up while minimizing disturbance to the soil systems. The excavation of intact roots was generally easy because the root systems of the young seedlings grown in the sandy soil were small. However, since some of the more elongated roots of *Q. variabilis* seedlings were broken during excavation, ten seedlings without any damage were sampled per plot in March 2012, followed by five seedlings per plot in March 2013. The samples were separated into shoot and root components after washing. The soil-free samples were oven-dried at 65 °C to a constant weight. The biomass (kg m^{-2}) was

calculated by the mean dry weight per seedling (g tree^{-1}) and the number of seedlings in the plots (tree m^{-2}).

2.4 Statistical analysis

A three-way analysis of variance (ANOVA) was used to examine the effects of experimental warming, species, year, and their interaction on soil temperature, water content, plant biomass, SCO_2, and R_S. A two-way ANOVA was used to analyze the effects of species and month on the response of R_S to warming. In order to assess the warming effect, we used the differences in measurements between the control and warmed plots and the response ratio of R_S to warming. The response ratio was defined as the percentage increase ratio (%) = (R_S warmed / R_S control − 1) × 100, where a negative value indicates a negative effect. To correct for differences caused by uneven soil temperature increases across the different species or different months, we normalized the warming effect to provide a value per 1 °C increase by dividing the response ratio by the actual temperature increase. To measure the sensitivity of R_S to seasonal temperature, we used the exponential function $R_S = a \exp^{bT}$, where R_S is soil respiration, T is soil temperature, and the coefficient a is the intercept of soil respiration when the temperature is zero. The coefficient b is used to calculate the Van't Hoff's temperature coefficient ($Q_{10} = \exp^{10b}$), which expresses the increase in R_S with a 10 °C increase in temperature during measurement (Curiel Yuste et al. 2004). Linear regression analysis was used to examine the relationships between soil water content vs. R_S and soil water content vs. the warming effect on R_S. Tukey's studentized range test or Student's t tests were used to analyze the differences in the SCO_2, R_S, and Q_{10} among treatment plots. All significance levels were quoted at a 95 % confidence level ($P < 0.05$). All statistical analyses were performed using SAS 9.4 (SAS Institute Inc., USA).

3 Results

3.1 Soil temperature and soil water content

The experimental open-field warming system significantly increased both air and soil temperatures (Table 1). Warming increased the annual mean air temperature by 2.5 °C in 2011 and by 2.0 °C in 2012. The actual degree of warming was lower than the target air temperature increase of 3 °C, and this discrepancy can be explained by the weather conditions and the seedling canopies. Warming increased the annual mean soil temperature by 1.1 and 1.3 °C at the *Q. variabilis* plot and by 2.4 and 1.5 °C at the *P. densiflora* plot in 2011 and 2012, respectively ($P < 0.001$; Table 2, Fig. 2a, b). Some interactions among warming treatment, species, and year were also significant for soil temperature. In comparison to the

Table 1 Results of a three-way ANOVA showing the P values for the response of soil temperature (T_S), soil water content (SWC), root and shoot biomass, SCO_2, and R_S to species type, warming, and their interaction

Factor	T_S	SWC	Root	Shoot	SCO_2	R_S
Warming (W)	<0.0001[***]	0.0328[*]	0.5913	0.5648	0.7680	<0.0001[***]
Species (S)	0.0153[**]	0.0021[**]	<0.0001[***]	0.0070[**]	0.0078[**]	<0.0001[***]
Year (Y)	<0.0001[***]	0.6748	<0.0001[***]	0.0004[***]	0.0452[*]	–
W × S	0.0075[**]	0.2906	0.2801	0.4939	0.5395	0.0098[**]
W × Y	0.1442	0.9299	0.7701	0.6665	0.8498	–
S × Y	0.0248[*]	0.8927	0.0005[***]	0.0287[*]	0.0849	–
S × W × Y	0.0498[*]	0.9133	0.8562	0.6306	0.8810	–

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

consistent differences in air temperature between the control and warmed plots, the warming effects on soil temperature fluctuated with season due to the interception of infrared heat by broad leaves of *Q. variabilis* or needle foliage of *P. densiflora*. This shield effect on soil temperature was higher at the *Q. variabilis* plot than at the *P. densiflora* plot (Table 2).

Although warming significantly affected soil water content (Table 1), the annual mean soil water content did not significantly differ between the control and warmed plots of either species in either year (Table 2). Warming slightly decreased mean soil water content during all days without precipitation in all plots (8.2 vol% in the control plots and 7.2 vol% in the warmed plots at the *Q. variabilis* plot, versus 6.6 vol% in the control plots and 5.5 vol% in the warmed plots at the *P. densiflora* plot; Table 2). The decrease in soil water content was less pronounced at the *Q. variabilis* plot (12 %) than the *P. densiflora* plot (17 %). These differences may be attributed to the differences in soil temperature or transpiration. In

addition, soil water content was directly influenced by rainfall events (Fig. 2c).

Figure 3a shows the seasonal variation in actual warming effect on air temperature around the canopy surface, on soil temperature, and on soil water content. The differences in soil temperature were lower than those of air temperature for both species. However, there was less difference in the leaf expansion period and winter than in the leaf maturity period, and the increase in soil temperature was lower in the *Q. variabilis* plot than the *P. densiflora* plot.

## 3.2 Response of R_S to warming

Warming significantly affected R_S and there was also a significant interaction between warming and species type (Table 1). Warming significantly enhanced mean R_S by 29 % at the *Q. variabilis* plot and by 22 % at the *P. densiflora* plot (Table 2). During the 2011 measurements, the average R_S rate

Table 2 Annual mean air and soil temperature, soil water content, soil CO_2 efflux (R_S) and concentration (SCO_2), and plant biomass (shoot and root) in the control and warmed plots planted with *Q. variabilis* and *P. densiflora* seedlings in 2011 and 2012. The value represents the mean ± 1 standard error ($n = 4$)

Year	Variables	*Q. variabilis*				*P. densiflora*			
		Control	Warmed	W–C (%[a])	P value	Control	Warmed	W–C (%)	P value
2011	Air temperature (°C)	12.4 ± 0.2	14.9 ± 0.6	+2.5 (+20)	<0.0001[***]	–	–	–	–
	Soil temperature (°C)	14.4 ± 0.1	15.5 ± 0.3	+1.1 (7)	0.0071[**]	14.4 ± 0.1	16.8 ± 0.2	+2.4 (+17)	<0.0001[***]
	Soil water content (%)	9.0 ± 0.8	8.6 ± 0.2	−0.4 (−4)	0.6325	7.5 ± 0.8	7.1 ± 0.3	−0.4 (−5)	0.6267
	R_S (μmol CO_2 m^{-2} s^{-1})	3.38 ± 0.27	4.37 ± 0.18	+0.99 (+29)	0.0090[**]	2.87 ± 0.16	3.50 ± 0.15	+0.63 (+22)	0.0105[*]
	Annual mean SCO_2 (μmol mol^{-1})	3158 ± 191	3532 ± 332	+374 (+12)	0.3664	3061 ± 333	2977 ± 236	−84 (−3)	0.8437
	ΔSCO_2 (Nov–Apr)	1100 ± 80	1309 ± 372	+209 (+19)	0.6017	970 ± 0.021	931 ± 189	−39 (−4)	0.7005
	Shoot biomass (kg m^{-2})	0.35 ± 0.07	0.49 ± 0.14	+0.14 (+40)	0.4125	0.27 ± 0.02	0.23 ± 0.02	−0.04 (−15)	0.2532
	Root biomass (kg m^{-2})	1.02 ± 0.15	1.26 ± 0.18	+0.24 (+24)	0.3493	0.23 ± 0.01	0.19 ± 0.01	−0.04 (−17)	0.0595
	Shoot + root	1.38 ± 0.21	1.75 ± 0.32	+0.37 (+27)	0.3669	0.50 ± 0.02	0.42 ± 0.03	−0.08 (−16)	0.0631
2012	Air temperature (°C)	11.8 ± 0.1	13.8 ± 0.1	+2.0 (+17)	<0.0001[***]	–	–	–	–
	Soil temperature (°C)	12.7 ± 0.1	14.0 ± 0.3	+1.3 (10)	0.0035[**]	12.6 ± 0.2	14.1 ± 0.2	+1.5 (+12)	0.0010[***]
	Soil water content (%)	7.5 ± 0.4	7.8 ± 0.1	−0.4 (−4)	0.1185	7.6 ± 0.3	6.8 ± 0.4	−0.4 (−5)	0.5534
	Annual mean SCO_2 (μmol mol^{-1})	4416 ± 646	4587 ± 428	+171 (+4)	0.8328	3166 ± 407	2977 ± 236	−189 (−6)	0.8822
	ΔSCO_2 (Nov–Apr)	1532 ± 76	1437 ± 153	−95 (−6)	0.6020	1181 ± 73	1193 ± 169	+12 (+1)	0.9502
	Shoot biomass (kg m^{-2})	2.53 ± 0.66	3.41 ± 1.42	+0.88 (+35)	0.5996	1.29 ± 0.08	1.20 ± 0.08	−0.09 (−7)	0.4595
	Root biomass (kg m^{-2})	4.82 ± 1.07	5.45 ± 1.27	+0.63 (+13)	0.7141	1.03 ± 0.09	1.12 ± 0.05	+0.09 (+9)	0.3842
	Shoot + root	7.35 ± 1.72	8.86 ± 2.65	+1.33 (+21)	0.6499	2.19 ± 0.15	2.32 ± 0.12	+0.13 (+6)	0.9825

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

[a] Percentage increase (+) or decrease (−)
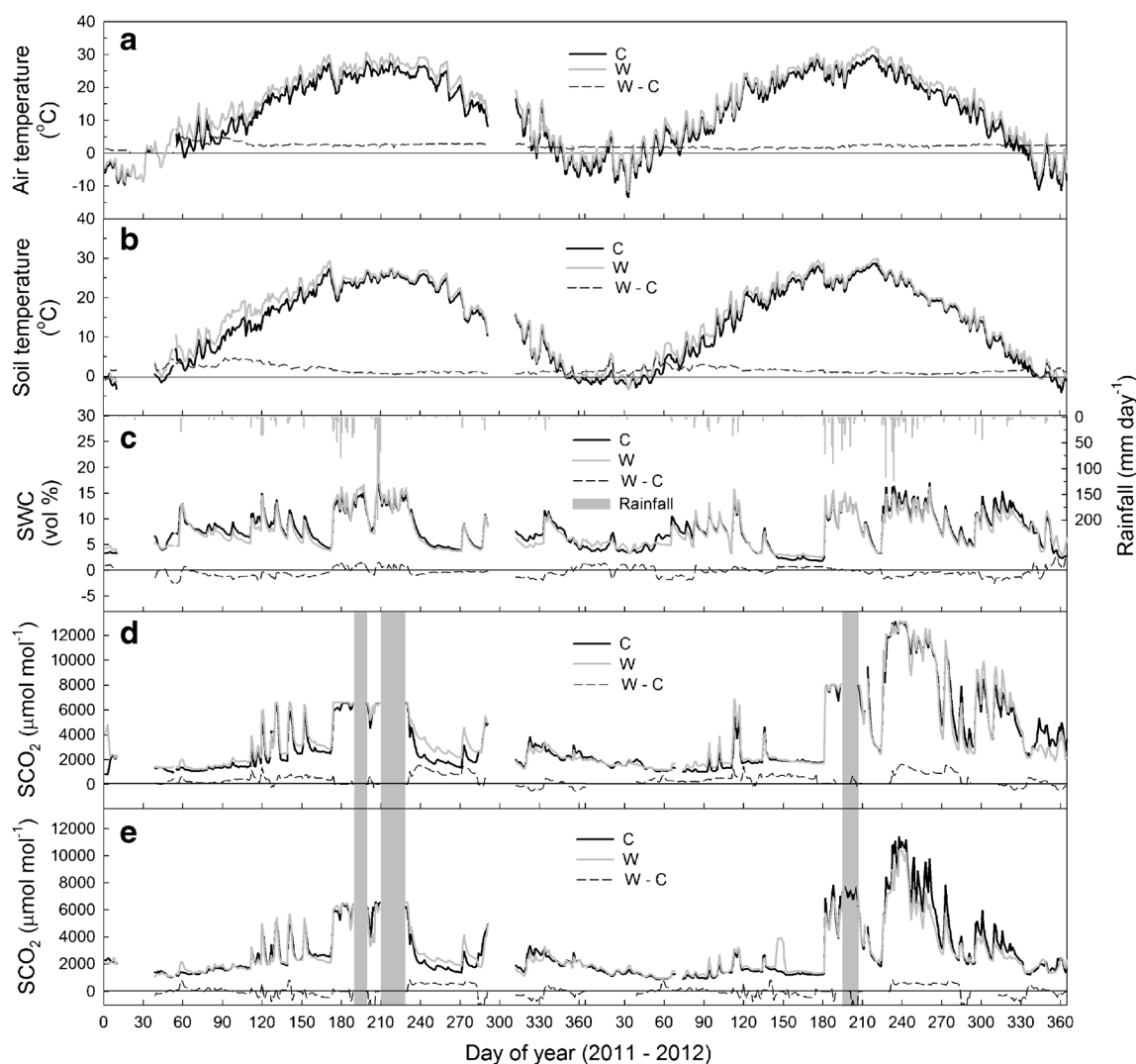
Fig. 2 Seasonal variations in the daily mean **a** air temperature ($n = 4$) at the *Q. variabilis* plots; **b** soil temperature ($n = 8$); **c** volumetric soil water content ($n = 8$) and rainfall at the all plots, and the seasonal variation in soil-air CO_2 concentration ($n = 4$) at the **d** *Q. variabilis* and **e** *P. densiflora* plots in 2011 and 2012. *Black and gray* lines indicate the control and warmed plots, respectively. *Dashed lines* show the differences in air and soil temperatures, soil water content, and SCO_2 between the control and warmed plots. The *gray bars* in **d** and **e** indicate missing SCO_2 data

($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) was significantly higher in the warmed plots than in the control plots for both *Q. variabilis* (3.38 ± 0.27 in the control plots and 4.37 ± 0.18 in the warmed plots) and *P. densiflora* (2.87 ± 0.16 in the control plots and 3.50 ± 0.15 in the warmed plots; Table 2).

R_S ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) exhibited seasonal variation ranging from 2.1 to 7.8 in the control plots and from 1.6 to 11.1 in the warmed plots at the *Q. variabilis* plot, and from 1.9 to 6.2 in the control plots and from 2.2 to 7.0 in the warmed plots at the *P. densiflora* plot throughout the growing season (Fig. 3b, c). Mean R_S increased from early in the growing season, reached its peak in August, and gradually decreased from September to November at both the *Q. variabilis* and *P. densiflora* plots.

Figure 4 presents the seasonal variation in the difference in R_S between the control and warmed plots, as well as the increase ratio of R_S normalized by 1 °C soil warming in the study plots. At the *Q. variabilis* plot, the warming effect on R_S gradually increased from June and peaked in August, while the warming effects on R_S at the *P. densiflora* plot peaked in June and subsequently decreased thereafter. For both species, the differences in R_S were negative in September, and then became positive again in October and November. Positive effects of warming on R_S were generally observed across the seasons for both species. However, a negative effect of warming on R_S was observed at the *P. densiflora* plot in September (Figs. 3c, 4).
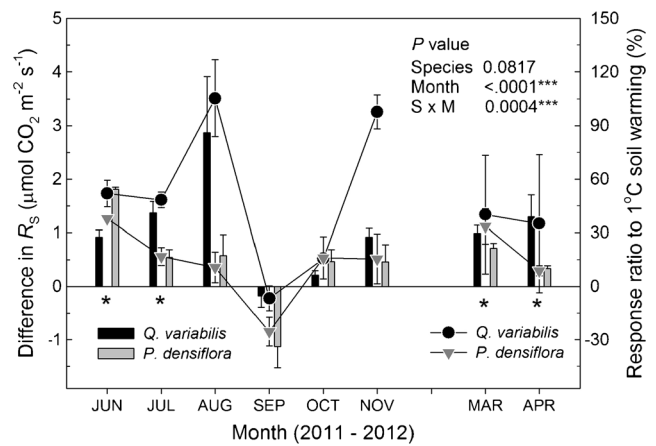
3.3 Relationships between R_S and soil temperature, and soil moisture content

R_S was correlated with soil temperature in the control and warmed plots for both species ($P < 0.001$; Table 3). The annual
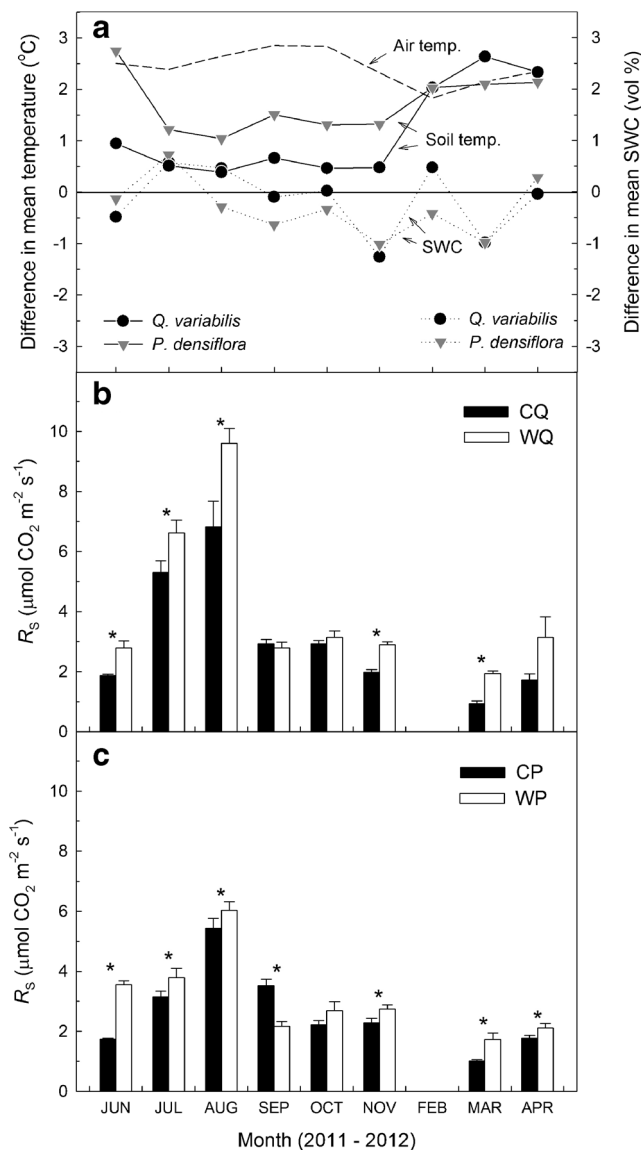
Fig. 3 Seasonal variation in **a** differences in the mean air (*dashed line*) and soil temperature (*solid line*), and volumetric soil water content (*dotted line*) between the control and warmed plots at the *Q. variabilis* (*black*) and *P. densiflora* (*gray*) plots and mean soil CO_2 efflux in the control and warmed plots at the **b** *Q. variabilis* and **c** *P. densiflora* plots from June 2011 to April 2012. *Vertical bars* indicate the mean ± 1 SE (*n* = 4) and the *asterisks* denote significant differences at the *P* = 0.05 level. *CQ* (control *Q. variabilis* plot), *WQ* (warmed *Q. variabilis* plot), *CP* (control *P. densiflora* plot), *WP* (warmed *P. densiflora* plot)

Fig. 4 Difference in soil CO_2 efflux (R_S) between the control and warmed plots (*bars*) and the response ratio (%, *points*) of R_S to warming between the control and warmed plots from June 2011 to April 2012 at the *Q. variabilis* (*black*) and *P. densiflora* (*gray*) plots. Values represent the mean ± 1 SE (*n* = 4). Results from a two-way ANOVA factoring in species and months are reported in the figure. *Asterisks* denote significant differences (*P < 0.05, ***P < 0.001)

with soil water content across all the plots ($R^2 = 0.48$, $P = 0.013$; Fig. 5b), enabling the identification of the negative effects of warming on R_S at low soil water levels at the *P. densiflora* plots.

3.4 Response of soil-air CO_2 concentration to warming

Warming did not affect mean SCO_2 for both species; however, significant differences between the two species were observed (Table 1). Mean SCO_2 (μmol mol^{-1}) demonstrated seasonal variations, ranging from 907 to 12,297 in the control plots and from 1082 to 12,397 in the warmed plots for *Q. variabilis*, and from 888 to 11,383 in the control plots and from 937 to 10,381 in the warmed plots for *P. densiflora* (Fig. 2d, e). SCO_2 notably fluctuated during the growing season, especially during the periods with rain events.

Figure 6 illustrates one of the clearest diurnal variations of SCO_2 with soil temperature, soil water content, and rainfall during a representative period (3 days) of the growing season. Generally, soil temperature and SCO_2 exhibited sinusoidal variation. SCO_2 dramatically increased with increasing soil water content caused by rainfall, following a time lag. At the same time, significant warming effects on SCO_2 were observed at both species (Fig. 6c, d). For instance, the daily mean SCO_2 on 29 September was 89 % higher in the warmed plots than in the control plots for *Q. variabilis*, and 55 % higher in the warmed plots than in the control plots for *P. densiflora* ($P < 0.05$). In general, soil temperature increased from 6:00, reached its maximum between 15:00 and 16:00, and gradually decreased thereafter, while SCO_2 reached a minimum during the daytime in both the control and warmed plots (Fig. 6c, d).

temperature sensitivity of R_S was higher at the *Q. variabilis* plot than at the *P. densiflora* plot ($P < 0.05$), but was not affected by warming. The Q_{10} values calculated from all the measurements were 2.82 for the control plots and 2.46 for the warmed plots at the *Q. variabilis* plots, and 1.98 for the control plots and 1.81 for the warmed plots at the *P. densiflora* plots (Table 3). R_S was positively correlated with soil water content for both *Q. variabilis* plots ($R^2 = 0.61$, $P = 0.003$) and *P. densiflora* plots ($R^2 = 0.37$, $P = 0.013$) in 2011 (Fig. 5a). In addition, the effect of warming on R_S was positively correlated

Table 3 The temperature sensitivity of R_S derived from the relationship between soil temperature and soil respiration ($R_S = a\exp^{bT}$) in the control and warmed plot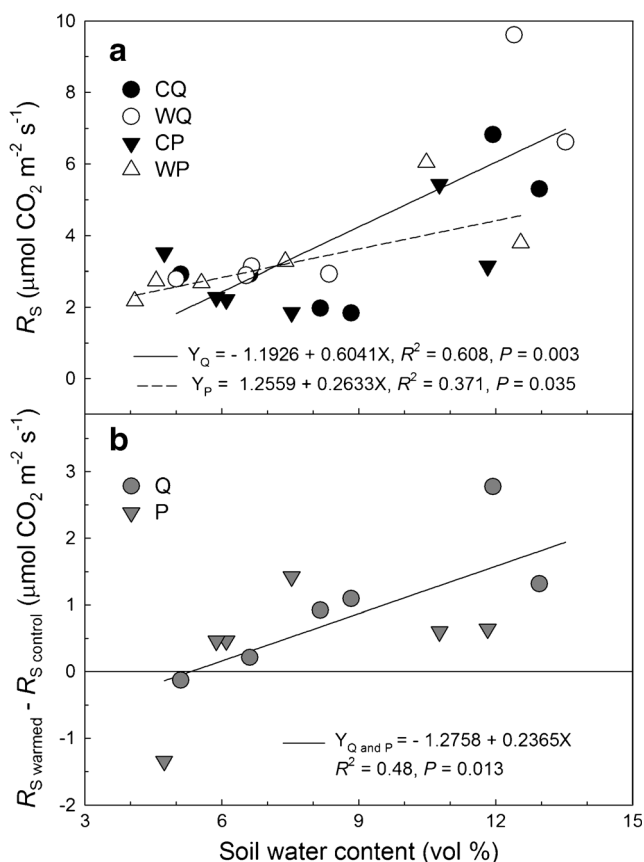s. *a*, basal respiration rate; *b*, coefficient values for the calculation of the Q_{10} values ($Q_{10} = \exp^{10b}$). Means ± 1 SE ($n = 4$) within a row that differ in their letters are significantly different at $P < 0.05$

Species	*Q. variabilis*		*P. densiflora*	
Treatment	Control	Warmed	Control	Warmed
a	0.440 ± 0.034B	0.710 ± 0.082AB	0.725 ± 0.060AB	0.925 ± 0.085A
b	0.105 ± 0.003A	0.090 ± 0.007A	0.068 ± 0.006B	0.060 ± 0.004B
Q_{10}	2.823 ± 0.083A	2.455 ± 0.007A	1.975 ± 0.103B	1.805 ± 0.082B
R^2	0.828	0.903	0.643	0.925
P	<0.001	<0.001	<0.001	<0.001

3.5 Plant biomass

Warming did not affect plant biomass significantly, while species type, year, and their interaction affected root and shoot biomass (Table 1). At the *Q. variabilis* plots, no significant difference in root and shoot biomass was observed between the control and warmed plots ($P > 0.05$), whereas at the

Fig. 5 Plots of **a** soil CO_2 efflux (R_S) against soil water content and **b** the difference in R_S between the control and warmed plots against soil water content for *Q. variabilis* (Q) and *P. densiflora* (P) species in 2011. These mean values are as in Figs. 3 and 4. The linear regressions were fitted to the data of the each species for **a** and all the data of the two species for **b**. CQ (control *Q. variabilis* plot), WQ (warmed *Q. variabilis* plot), CP (control *P. densiflora* plot), WP (warmed *P. densiflora* plot)

P. densiflora plots a trend towards decreased root biomass was observed in the warmed plots relative to the control plots only in 2011 ($P = 0.059$; Table 2). The root biomass was higher at the *Q. variabilis* plots than at the *P. densiflora* plots ($P < 0.001$). In 2011, total biomass values (shoot plus root) for the control and warmed plots were 1.38 kg m^{-2} and 1.75 kg m^{-2} for *Q. variabilis* and 0.50 and 0.42 kg m^{-2} for *P. densiflora*, respectively. Mean R_S increased with increase in root biomass ($R^2 = 0.69$) and total biomass ($R^2 = 0.73$). But the correlations across both species were not significant due to the limited amount of data ($P > 0.05$). Mean SCO_2 was positively correlated with root biomass (Fig. 7c, $R^2 = 0.99$, $P = 0.003$) and total biomass (Fig. 7d, $R^2 = 0.87$, $P = 0.007$) for both species in 2012.

4 Discussion

4.1 Stronger response of R_S to warming for *Q. variabilis* than for *P. densiflora*

In this study, warming stimulated the mean R_S rate by 29 and 22 % at the *Q. variabilis* and *P. densiflora* plots, respectively (Table 2). These response ratios were higher than the normalized mean response ratio (12 %) of R_S derived from experimental warming of 2 °C in temperate forests (Wang et al. 2014), supporting the observation that young tree seedlings in early development stages are more responsive to increasing temperature than are mature or old growth stands (Xu et al. 2012).

We hypothesized that the R_S response to a temperature rise with *Q. variabilis* seedlings would be stronger than with *P. densiflora* seedlings. Our study showed that the average effect of warming on R_S was higher at the *Q. variabilis* plot than at the *P. densiflora* plot, despite the warming effect on soil temperature being lower than for *P. densiflora*. Also, there was no significant increase in plant biomass for either species. The lower warming effect on *P. densiflora* seedlings may be related to the lower dependency of R_S to growth temperature than
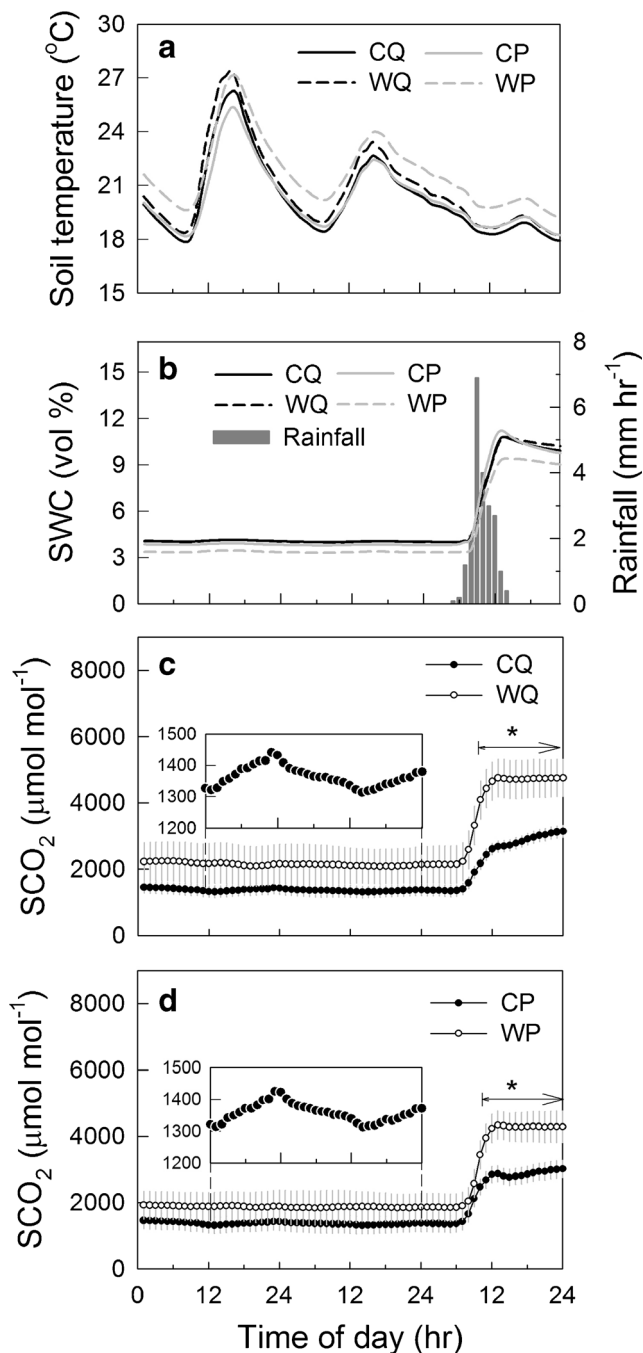
Fig. 6 Diurnal variations of hourly mean **a** soil temperature; **b** volumetric soil water content and rainfall and soil-air CO_2 concentration at the **c** *Q. variabilis* and **d** *P. densiflora* sites (27–29 September 2011). *CQ* (control *Q. variabilis* plot), *WQ* (warmed *Q. variabilis* plot), *CP* (control *P. densiflora* plot), *WP* (warmed *P. densiflora* plot). The *closed and open circles* indicate the control and warmed plots, respectively. Each value is the hourly mean ± 1 SE ($n = 4$). The *insets* in **c** and **d** present the *y*-axis on a finer scale before rainfall and the *asterisks* denote significant differences in SCO_2 between the control and warmed plots ($P < 0.05$)

Q. variabilis seedlings (Table 3). Way and Oren (2010) addressed why evergreen trees may be less responsive to growth temperature. The adaptation strategies of

evergreen trees are generally suited to resource-poor environments and thus evergreens have more conservative responses to changing environmental conditions, such as their trade-offs between nutrient retention and plant growth (Givnish 2002; Aerts 1995). At our *Q. variabilis* plot, the warming-induced R_S may have been affected by an increase in photosynthesis capacity, such as increases in leaf longevity (Han et al. 2014a), chlorophyll content, and photosynthesis rate (Jo et al. 2011) in the same year, even though biomass was not significantly changed by warming. In addition, the 1.1 °C increase in soil temperature could directly stimulate rhizospheric respiration. On the other hand, at the *P. densiflora* plot, the warming did not affect any physiological leaf traits such as leaf nitrogen concentration or chlorophyll content (Lee et al. 2013). If the warming decreased root respiration in association with a negative plant productivity response to warming (Li et al. 2013), the warming-induced increase in R_S may have resulted mainly from the increase in rhizospheric and heterotrophic respiration by 2.4 °C soil warming (Kuzyakov and Gavrichkova 2010). If warming increased root respiration without increase in plant biomass, these results could be explained by differences in C allocation strategies between plant growth and respiration in warming conditions and different temperature dependencies. In other words, increases in respiration and photosynthetic capacity do not necessarily lead to more plant growth if the C allocation was used by the plants more for respiration than growth. This study cannot explain further due to a lack of data. However, more studies comparing the potential changes in the carbon allocation strategies, stomatal conductances and other C-demanding processes such as root exudation, of different species will give us clear insight and a better understanding of the links aboveground and belowground C processes.

4.2 Different seasonal variations in warming effects on R_S between the two species

We found differences in the temporal variation of the warming effect between *Q. variabilis* and *P. densiflora* (Fig. 4). The different warming effects on R_S could be explained by species-specific temperature sensitivities reflecting differences in leaf phenology between deciduous and coniferous seedlings (Curiel Yuste et al. 2004). The annual Q_{10} value of R_S reflecting a temperature dependency to seasonal soil temperature was also significantly higher in the *Q. variabilis* plot than in the *P. densiflora* plot (Table 3). The effect of warming was mainly noticeable in August at the *Q. variabilis* site whereas in June at the *P. densiflora* site. Because the leaf unfolding stage for *Q. variabilis* seedlings continued until the end of May with a leaf chlorophyll content peak in July (Jo et al. 2011; Han et al. 2014a), this may have led to the

Fig. 7 Relationships between mean SCO$_2$ and root and total biomass (shoot + root) across both tree species in **a**, **b** 2011 and **c**, **d** 2012. *CQ* (control *Q. variabilis* plot), *WQ* (warmed *Q. variabilis* plot), *CP* (control *P. densiflora* plot), *WP* (warmed *P. densiflora* plot). The values indicate mean ± 1 SE (*n* = 4)
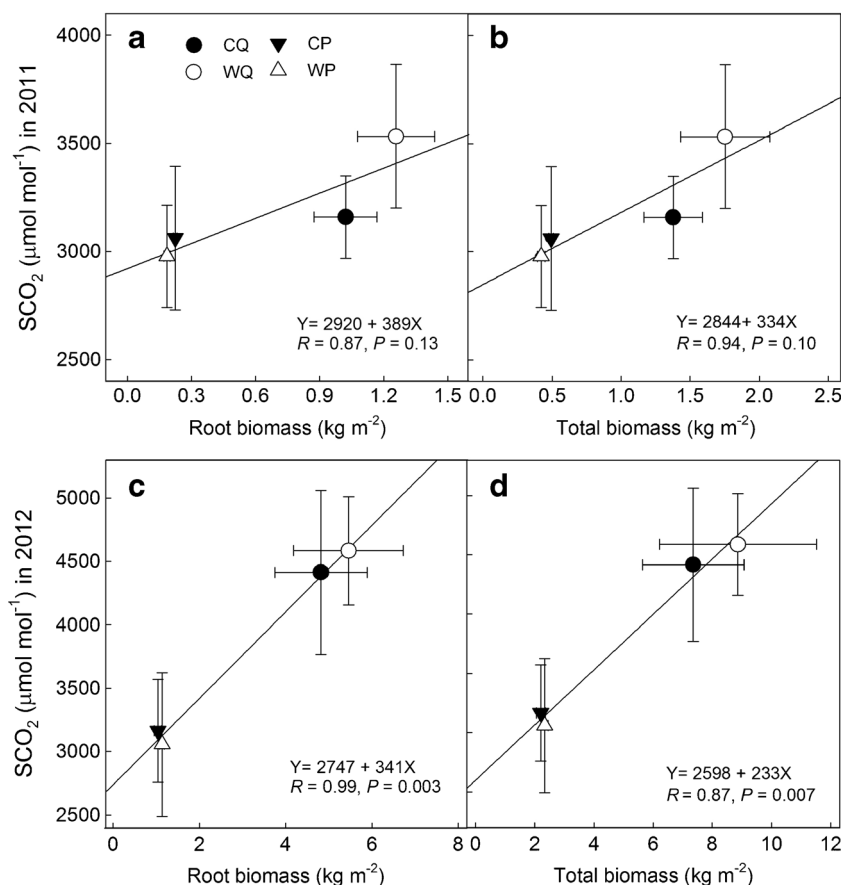
pronounced warming effect appearing later for *Q. variabilis* than for *P. densiflora*. Since root respiration, as a component of R_S, originates from leaf photosynthesis, the effect of warming on R_S for *Q. variabilis* seedlings may depend on leaf emergence and leaf area expansion (Du and Fang 2014). At this study site, warming increased leaf longevity in *Q. variabilis* seedlings by 27 days (Han et al. 2014a). In contrast, *P. densiflora* seedlings demonstrated no distinct leaf flushing and less variation in leaf chlorophyll content than did *Q. variabilis* seedlings from May to July (Lee et al. 2013). Therefore, the stronger effect of warming observed in *P. densiflora* seedlings during the early growing season may be due to the earlier C transition from needles to roots.

4.3 Soil water contents and the warming effect on R_S

We found a positive correlation between warming effects and soil moisture contents (Fig. 5b) suggesting that a severe drought before or after a rainy season might alter the warming effect. At our nursery site with sandy soil, the soil water contents were very low at the lower end of general soil water content range. Davidson et al. (1998) revealed a bimodal relation between R_S and volumetric water content in a temperate mixed hardwood forest, showing a positive correlation with a steep slope during the peak of the drought in August and

September. However, the dependency of R_S on soil water content that has been identified across studies is inconsistent due to complex mechanisms that are involved in moisture regulations of CO$_2$ production and transport processes (Luo and Zhou 2006), nursery warming experiments with wider ranges in soil water content should be considered. A recent study by Jarvi and Burton (2013) reported that soil warming increased root respiration rates when soil moisture was enhanced by the addition of water through rainfall. In our study, the mean soil water content during R_S measurement in September was down to 4 vol% (Fig. 2c) and the negative effect on R_S was less pronounced at the *Q. variabilis* plot than at the *P. densiflora* plot. If the negative effect on R_S is attributed to a reduction in plant growth associated with warming-induced drought, the *Q. variabilis* seedlings might be more water-stress tolerant than *P. densiflora* seedlings (Schwanz and Polle 2001). After rainfall, the positive effect of warming on R_S in the seedlings of both species was observed in October and November (Fig. 4). Because prolonged drought decreases heterotrophic respiration and photosynthetic capacity, warming-induced severe drought might offset the effect of increasing temperature on R_S (Borken et al. 2006; Misson et al. 2010; Xu and Baldocchi 2003). Therefore, further studies on the response of R_S to long-term warming combined with precipitation manipulation are needed.

4.4 Responses of plant biomass and SCO_2 to warming

In this study, warming did not significantly increase the biomass of *Q. variabilis* seedlings (27 %, *P* = 0.367). Intraspecific competition during shoot growth among *Q. variabilis* seedlings may cause large variations in biomass within a single plot. A meta-analysis by Lin et al. (2010) reported that warming generally increased both above and belowground biomass of woody plants by 26.7 %, although these changes depended on tree species, the level of warming, and the experimental period. According to Way and Oren (2010), the growth of deciduous trees is more responsive to increasing temperatures than that of evergreen trees. Specifically, the average response of growth variables (e.g., shoot height, stem diameter, and biomass) to a 3.4 °C increase in growth temperature was positive for deciduous trees and negative for evergreen trees. However, more species should be considered when determining the response of broader functional types to warming (Fisichelli et al. 2014; Han et al. 2014b). In our study, a trend towards slightly decreased root biomass was observed in the warmed plot of *P. densiflora* seedlings in 2011 (17 %, *P* = 0.059; Table 2). Decrease in growth rate or the change in C allocation can occur when warming-induced increases in respiration rate are greater than that in C assimilation rate due to photosynthesis (Kramer et al. 2000). Similar responses were also observed in the effect of warming on SCO_2. No significant difference in mean SCO_2 between the control and warmed plots was identified. However, we found a positive correlation between plant biomass and mean SCO_2 across the control and warmed plots of the two species (Fig. 7c, d). These results suggest that SCO_2 concentration could be a useful indicator of the release of C from the rhizosphere when significant changes in plant production due to warming would be expected. The SCO_2 concentration fluctuated markedly in comparison to previous studies (e.g., Tang et al. 2003; Yonemura et al. 2013). In particular, SCO_2 demonstrated a sensitive response to rainfall on diurnal time scales (Fig. 6). This may reflect the rapid water dispersion in the sandy soil. On the other hand, significant differences in SCO_2 between the control and warmed plots were observed after rainfall, following a time lag (Fig. 6c, d). Therefore, further studies are required to determine SCO_2 sensitivity to air-filled porosity and associated gas diffusion rates, as well as the effects of the soil depth at which sensors are located on the measurement of SCO_2.

5 Conclusions

Warming significantly increased mean R_S in both *Q. variabilis* and *P. densiflora* plots, but did not influence plant biomass in either species. Warming-induced increase in R_S did not seem to be directly linked to plant biomass, but the positive correlation between biomass and SCO_2 in the wide range of the plant biomass of the two species shows that SCO_2 may be useful index to access the warming effect on plant growth when its remarkable changes would be observed. In addition, R_S was more responsive to warming for *Q. variabilis* seedlings than for *P. densiflora* seedlings. If this result could be repeated at multiple developmental stages in future research, such different responses would imply that, in a warmer climate in Korean forests, *Q. variabilis* would accelerate its belowground C turnover more than *P. densiflora*. The warming effects on R_S also varied seasonally for both species showing that drier soil conditions would lead to a less or negative response of R_S to increasing temperature. This study shows that differences in seasonal variation in the response of R_S to temperature rises reflect differences in leaf phenology between deciduous and evergreen trees. This field-based evidence would contribute to accurate future predictions of the soil C cycle under climate change.

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