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Characteristics of stem respiration in black spruce (*Picea mariana*) stand, interior Alaska

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ABSTRACT

Boreal forests account for roughly one third of the carbon sequestered in terrestrial ecosystems, and the high-latitude boreal ecosystem they make up has been consequently vulnerable to recent climate change. This study investigated stem respiration of Alaska dominant black spruce trees in interior Alaska during the growing season of 2007. The continuous measurement of stem respiration was conducted in black spruce trees of four different ages (4.3, 7.2, 9.8, and 13.5 cm in diameter at breast height (DBH)) in interior Alaska, using a CO_2 analyzer, a 12-V pump, chambers, and a data-logger. Mean stem respiration is 0.014 ± 0.006 mg CO_2 m^{-2} s^{-1} (range 0.003–0.039 mg CO_2 m^{-2} s^{-1}) in different aged four black spruce trees, indicating remarkably temporal variations in stem respiration with temperatures in air and stem. We found that metabolism is 1.5-fold higher in the younger black spruce tree than in the older. Temperatures in air and stem are significant regulators in regulating stem respiration. The stand-level annual stem respiration simulated by Q_{10} value based on air temperature is 73.9 g CO_2 m^{-2}, corresponding to 5.0% of the ecosystem respiration (Re) estimated by eddy covariance tower in 2007. Our findings demonstrate that stem respiration is a significant component in the scale-up of the regional carbon budget in a black spruce forest of interior Alaska.

1. Introduction

Currently, high-latitude terrestrial ecosystems are at risk from increasing ambient temperatures (AMAP, 2011). Northern boreal forests represent approximately 35% of the world's permafrost area, and also contain approximately 66% of the world's forest soil carbon pools (Kasischke and Stocks, 2000). Recent studies also suggest a browning phenomenon in boreal forests, which has weakened the metabolic response to drastic climate change within interior Alaska (Verbyla, 2008; Parent and Verbyla, 2010). Meanwhile, stem respirations of boreal forests are sensitive to changes in climate and environment, leading to modulate the source capacity of atmospheric carbon (Ryan et al., 1995, 1997; Lavigne, 1996; Lavigne and Ryan, 1997). Stem respirations have contributed to 25–50% of ecosystem respiration in northern coniferous forests and deciduous forests (Edwards et al., 1981, Lavigne, 1996; Lavigne and Ryan, 1997). Thus, stem respiration is significant for both contributing to the carbon budget (Damesin et al., 2002), and for constructing the land surface model in northern coniferous forests (Ryan and Waring, 1992), which depends on parameters in environments and ecophysiologies such as temperature, PAR (photosynthetically active radiation), DBH (diameters at breast height), sapwood volume/surface area, and so on (Ryan et al., 1995; Lavigne, 1996; Carey et al., 1997; Lavigne and Ryan, 1997; Ceschia et al., 2002; Zha et al., 2004; Lavigne et al., 2004; Acosta et al., 2008). Stem respiration from non-photosynthetic organs has gained forest carbon attention since CO_2 emission was mainly determined by respiration instead of total photosynthesis by green organs (Janssens et al., 2001).

Eddy covariance tower observation is a beneficial tool for consecutively determining the ecosystem carbon cycle's photosynthesis and respiration at hourly, daily, weekly, monthly, annual and inter-annual periods (Law et al., 1999; Aubinet et al., 2002; Baldocchi, 2003; Ueyama et al., 2014). Nevertheless, eddy covariance methods do not support direct information from each compartment contribution, and are difficult to evaluate across heterogeneous regions due to peculiar variations in the influencing footprint on a space-time scale. Hence, stem respiration plays a significant part in elucidating differences and

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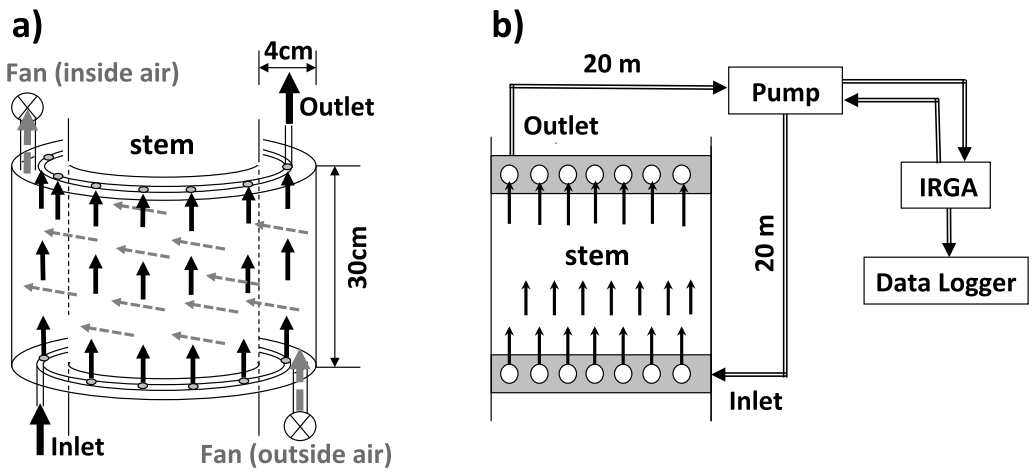

Fig. 1. Scheme for stem respiration measuring system. (a) Grey dashed bevel arrows denote exchange of inside and outside air by two fans of the top and bottom under no measurement, and vertical solid arrows show the transport of sample air emitted from the stem surface by pump for CO_2 analysis after closing the two fans and measuring. (b) CO_2 concentration in transported air is measured by the IRGA (Infra-Red Gas Analyzer) for determination of CO_2 concentration gradient for 7.5 min, and measured data is stored to the data logger.

variations in ecosystem respiration (Ryan et al., 1995; Law et al., 1999; Damesin et al., 2002; Shibistova et al., 2002; Tang et al., 2008).

Interpreted stem respiration rates are affected by the spatiotemporal intensity of measurement, and also by the differences in observing methodology. For instance, methodological factors such as an active cross-section of the chamber, measuring frequency (e.g., hourly, daily, monthly, seasonal and annual), and stem respiration-measuring system type (e.g., manual or automated type) may affect each respiration computation (Ryan et al., 1995; Damesin et al., 2002; Vose and Ryan, 2002; Zha et al., 2004). Widely recognized, different methodologies are used for different purposes, and manual chamber systems are traditionally used for capturing spatial heterogeneity, while automated chamber systems offer much improved measurement frequency during snow-free periods (Zha et al., 2004; Kim et al., 2016). To a large extent, the degree to which measured respirations are representative of reality depends on a half-hour interval and spatial coverage within same boreal forest trees, with the automated chamber system used in this study.

Stem respiration is directly dependent on change in temperature, well known as the most significantly environmental parameter in regulating stem respiration, estimating carbon budgets in response to climate change, and validating ecosystem productivity models and land surface models on local and region scales (Paembonan et al., 1991; Ryan et al., 1995; Lavigne, 1996; Lavigne and Ryan, 1997; Xu et al., 2000; Vose and Ryan, 2002; Zha et al., 2004; Harris et al., 2008; Rossi et al., 2011; Lugo et al., 2012).

Measurement of stem respiration is important for improving our understanding of ecosystem carbon cycling and budget, which influences the carbon and energy balance in the ecosystem and contributes to feedbacks driving future climate change (Xu et al., 2000). Stem respiration as a percentage of the aboveground carbon budget is estimated to comprise anywhere from 9%, in a 50-year-old stand of Scot pine (Zha et al., 2004), to as much as 13% (Ryan and Waring, 1992) in a 245-year-old stand of lodgepole pine. Moreover, since forest ecosystems are very finely balanced between carbon sources and carbon sinks (Ryan et al., 1997), it has become crucial to improve the accuracy of models used for estimating forest carbon budgets, and thus for improving our knowledge of stem respiration processes (Ceschia et al., 2002). Further, measuring the stem respiration process and understanding what regulates it are essential steps in understanding regional and global carbon balances, and in modeling the CO_2 exchange between forests and the atmosphere (Zha et al., 2004).

Black spruce communities, a dominant (39–44%) stand in the interior boreal forest, are widely distributed in interior Alaska, and underlain here by discontinuous permafrost (Barney and Stocks, 1983; Viereck et al., 1992). Alaska black spruce communities typically occur at cold, poorly drained, nutrient-poor sites with a shallow permafrost layer; hence, and productivity is typically low (Viereck et al., 1992).

These questions and requirements have been addressed by continuously monitoring the stem respiration rate of a black spruce tree (*Picea mariana*) in interior Alaska during the growing season of 2007. Our objectives are to 1) determine the response by stem respiration from differently aged black spruce trees to temperatures during the growing season; 2) examine intra-annual changes in stem respiration rate, simulated by Q_{10} value based on air temperature; and 3) evaluate the contribution from stem respiration rate to Re (ecosystem respiration; $gCO_2\ m^{-2}\ d^{-1}$), estimated by eddy covariance tower in a black spruce forest, Interior Alaska.

2. Materials and experimental methods

2.1. Research sites

The research site was located on the western ridge of the University of Alaska Fairbanks, in interior Alaska (64°51′N, 147°50′W, 166 m.a.s.l.). This site represents a typical boreal black spruce forest (*Picea mariana*), at which mean height was 6.6 m within a 60 × 60 m plot. Black spruce density was 3290 tree/ha, according to a forest census survey that measured bottom diameter (D_o) and DBH (diameter at breast height: 1.3 m high) of black spruce trees. Within the plot, 1183 trees were alive and 43 were dead. Average D_o and DBH were 6.6 ± 3.2 cm and 4.6 ± 2.5 cm, respectively. Ueyama et al. (2014) reported ages ranging from 35 to 120 years old at the neighboring site, based on tree-ring investigation.

Stem respiration of these black spruce trees was monitored during the growing season of 2007. The four targeted black spruce trees were 4.3, 7.2, 9.8, and 14.5 cm in DBH, and 3.6, 6.1, 9.2, and 10.3 m high, respectively, representing four differently aged trees. However, this study could not determine the exact age spans for the four trees, as we did not cut holes in the stems for dating. Rosner (2004) found that height-age trends of black spruce showed similar growth rates but variations in ages at breast height, indicating a positively good linear relationship between height and ages at breast height. Also, Wirth et al. (1999) reported linear relationships for average tree height-stand age and for DBH-stand age in four chronosequence of Central Siberian *Pinus sylvestris* stands.

The forest floor is made up of tussocks, vascular plants, shrubs, sphagnum and feather mosses, and lichen (e.g., *Betula glandulosa, Ledum palustre, Vaccinium vitis-idaea, Carex lugens, Sphagnum* spp., *Thuidium abietinum, Cladina stellaris*) over a discontinuous permafrost regime. Annual mean air temperature was −2.0 °C, and mean temperature in July was 17.3 °C, representing the maximum temperature for this area in the last forty-five years. Annual mean precipitation was 290 mm, and the mean precipitation of 47 mm from August was also the highest for this area in the past forty-five years. During the growing season of May 1

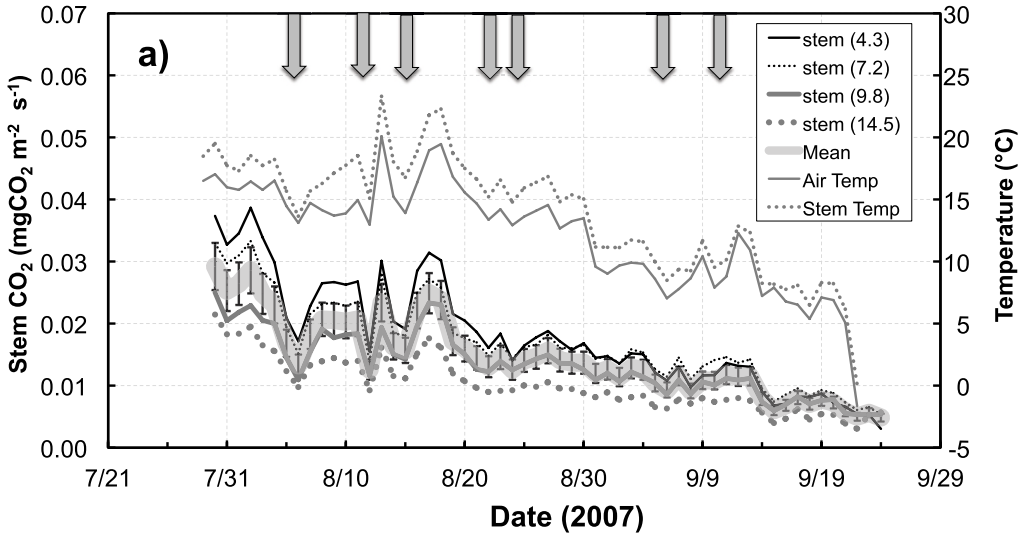

Fig. 2. Temporal variations in stem respirations of four black spruce trees with mean (thick grey line) with error bars, as well as temperatures in air (grey solid line) and soil (grey dotted line), and heavy precipitation events (downward grey arrows). Rainy events led to decreased stem respiration and temperature in the mid-growing season.

to September 30 of 2007, mean air temperature and precipitation were 13.6 °C and 243 mm, respectively, corresponding to 84% of annual precipitation.

2.2. Determination of stem respiration and environmental parameters

The automated chamber system used for stem respiration (SR) consists of 1) four stem chambers; 2) a control box, including a mini-pump (5 L min^{-1}, Enomoto Micro Pump Co., Japan), and a desiccant tube (3-cm inside diameter, 20-cm length) filled with Drierite (Fisher Scientific, USA); 3) an infrared gas analyzer (IRGA; Li-820, Licor, Nebraska, USA); and 4) two data loggers (CR-1000, Campbell Scientific Inc., Utah, USA) for storage of CO_2 concentration and environmental parameters. The scheme on the stem chamber installed at the DBH of the four trees is shown in Fig. 1. The body of the stem chamber was made of a transparent, high-density polyethylene (HDPE) film (35 cm high, 60 cm wide; 0.05 cm thick). The top and bottom parts of the chamber were packed with commercial self-sealing insulation foam, and then fixed with clear silicone and assorted cable ties to prevent outside air from entering the chamber inside. Each chamber had two fans at the top and bottom surfaces for the exchange of outside and inside air, with inlet tubing (0.6-cm diameter) on the bottom and an outlet at the top. When measurements were not conducted, inside air was exchanged with outside air by two fans before the determination (grey arrows; Fig. 1a). Top and bottom tubes in the inside chamber had twenty to thirty holes (0.3 cm in diameter), used to measure CO_2 concentration emitted from the overall surface of each stem (solid arrows; Fig. 1a–b). The two fans on the top and bottom were stopped, the upper and lower valves were closed, inside air was transferred to the CO_2 gas analyzer by the pump, and the change in CO_2 concentration was measured for 7.5 min, as shown in Fig. 1b. In order to remove the remnants of outside air and estimate the 'real' concentration gradient, the first one to 3 min of CO_2 concentration was discarded due to contamination by previous air samples in the tubing from chamber to analyzer. Stem respiration estimated hourly mean values at 30-min intervals. The chamber was 4 cm higher than the stem surface and 30 cm long, as shown in Fig. 1a. Although these four stem respirations were monitored from the end of July to the end of September, these data can be analyzed for characteristics in temporal variations and the contribution of stem respiration from the averaged four trees to ecosystem respiration (Re), measured from the eddy covariance tower.

Growing season environmental parameters measured temperatures of air and stem using two thermocouples (T type; Oregon Scientific Co., USA). Temperatures in air and stem were measured 1.5 m above the surface and 0.01 m below the stem bark, respectively.

Stem respiration (SR) is calculated using the following equation:

$$SR = (\Delta C / \Delta t) \times (V / A), \quad (1)$$

where SR is stem respiration (mg CO_2 m^{-2} s^{-1}), ΔC is the change in CO_2 concentration for measuring time (Δt, in seconds), and V and A are the volume and surface area of the chamber (m^3 and m^2), respectively. We computed the temperature's dependency on observed hourly stem respiration by fitting the following equation for temperatures of air and stem:

$$SR = \beta_0 \times e^{\beta 1 \times T}, \quad (2)$$

where SR is measured stem respiration (mg CO_2 m^{-2} s^{-1}); T is temperature (°C) in air and stem; and β_0 and β_1 are constants. This exponential relationship is commonly used to represent stem respiration as a function of temperature. Q_{10} is a measure of the change in reaction rate at intervals of 10 °C, and is based on Van't Hoff's empirical rule that a rate increase on the order of two to three times occurs for every 10 °C rise in temperature (Lloyd and Taylor, 1994). Q_{10} value was calculated thusly:

$$Q_{10} = e^{\beta 1 \times 10} \quad (3)$$

A reference value for R_{10} (stem respiration normalized to an air temperature of 10 °C; Kim et al., 2014) was then calculated as

$$R_{10} = R_i \, Q_{10}^{[(10-T)/10]}, \quad (4)$$

where R_i is simulated stem respiration (mg CO_2 m^{-2} s^{-1}) and T is air temperatures (°C). Using calculated values for Q_{10} and R_{10}, stem respiration was simulated on the basis of measured air temperature (Kim et al., 2014, 2016bib_Kim_et_al_2014bib_Kim_et_al_2016). This transformation was applied to meet the homoscedasticity condition (i.e., equal variance around the regression line for all values of the independent variable), which is required to perform regression using the Q_{10} function, as in equation (4). In order to estimate stem respiration for each tree, simulated stem respiration R_i (mg CO_2 m^{-2} s^{-1}) was calculated as

$$R_i = R_{10} / Q_{10}^{[(10-T)/10]}, \quad (5)$$

The parameters of the nonrectangular hyperbola function were determined daily, using a fifteen-day moving window and the least-squares method. Stem respiration (SR) was estimated using the following two models (Ueyama et al., 2014; Kim et al., 2016):

$$SR = R_0 \times Q_{10}^{(Ta,s/10)}, \quad (6)$$

$$SR = R_{ref} \times \left[\frac{E_0}{R_{gas}}\left(\frac{1}{T_k + T_{ref} - T_0} - \frac{1}{T_k + T_a - T_0}\right)\right], \quad (7)$$

where $T_{a,s}$ is air temperature and stem temperature, R_o represents stem respiration at 0 °C, and Q_{10} is the temperature sensitivity coefficient of stem respiration. R_{ref} is the stem respiration at T_{ref}, E_0 is the activation energy, and R_{gas} is the ideal gas constant. T_k, T_0, and T_{ref} are 273.15 K, 227.13 K, and 283.15 K, respectively (Lloyd and Taylor, 1994). We used the conventional Q_{10} model to estimate stem respiration, though we used the Lloyd and Taylor model equation (7) for uncertainty estimates—as Q_{10} exhibited clear seasonal variations, whereas E_0 showed no discernible seasonal variation. We also performed a one-way ANOVA (95% confidence level) for this data, using Microsoft Excel Data Analysis software. We used regression analysis to examine the relationship between stem respiration and environmental parameters.

3. Results and discussion

3.1. Temporal variations in stem respiration and environmental parameters

Temporal variations in daily stem respirations of four different aged black spruce trees (4.3-, 7.2-. 9.8-, and 14.5-cm diameter at DBH), as well as temperature in air and stem, during the growing seasons of 2007 are shown in Fig. 2. Daily mean stem respirations ±standard deviation of four black spruce trees were 0.020 ± 0.016, 0.018 ± 0.011, 0.015 ± 0.009, and 0.011 ± 0.008 mg CO_2 m^{-2} s^{-1}, respectively. That is, younger stems represented much higher respiration, representing more active metabolism (i.e., photosynthesis and respiration), relative to the old. Furthermore, black spruce trees showed a much slower growth rate than other species, despite being the dominant trees in the Alaska boreal forest (Barney and Stocks, 1983; Viereck et al., 1992). Alaska black spruce communities typically occur at poorly drained, nutrient-poor sites with a discontinuous permafrost layer; hence, their productivity is much lower relative to other stands (Viereck et al., 1992). Wolken et al. (2016) showed that the mean ring width of black spruce at different site levels (eg, Summit, Side slope, Toe slope, and Valley bottom) was 0.42 ± 0.04 mm yr^{-1}, in interior Alaska.

Average stem respiration ±standard deviation during 2007 was 0.014 ± 0.011 mg CO_2 m^{-2} s^{-1}, as shown in Fig. 2. Seasonal characteristics of stem respirations on the four trees showed up-and-down patterns during the growing seasons, reflecting dependency on daily air temperature. This pattern is also associated with the precipitation events during the growing season, as shown in Fig. 2. For instance, Zha et al. (2004) reported that stem respiration showed a much slower response to the temperatures in air and stem before, compared to just after, a rainfall event. However, this study has not shown any relationship between daily mean stem respiration and daily precipitation (not shown). Nevertheless, additional work is required to identify the relationship between hourly stem respiration and soil moisture.

Stem respiration of the 14.5-cm black spruce was higher than other black spruce trees below zero. When temperature rapidly dropped below zero after September 22, stem respiration from the old tree (14.5 cm) remained nearly constant relative to the others, possibly due to its relatively larger heat capacity against a sudden change in ambient temperature (Becker and Edwards, 1999; Gu et al., 2007). Unfortunately, winter stem respiration-measurement was not conducted during the snow-covered period because of degradation to the rubber-made diaphragm pump under the extremely cold environment of interior Alaska.

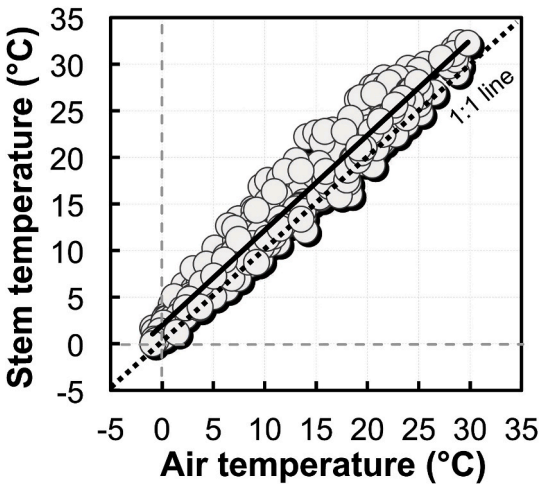

Fig. 3. Response from hourly stem temperature (ST) of black spruce tree to hourly air temperatures (AT). Solid and dotted lines indicate relationships between stem temperature and air temperature, and a 1:1 line, respectively. The equation is ST = 1.02 × AT + 1.99 (R^2 = 0.95; n = 1489) during the growing season.

Daily mean temperatures of air and stem ±standard deviation in four trees were 12.1 ± 7.8, and 13.3 ± 8.0 °C during the observation period of 2017, respectively. As shown in Fig. 2, in general, stem temperature was slightly higher than ambient temperature. Ambient temperature (AT) was linearly correlated to stem temperature (ST) in the black spruce trees, indicating $ST = 1.02 \times AT + 1.99$ ($R^2 = 0.95$; $p < 0.01$; $n = 1489$) during the growing seasons of 2007 (Fig. 3). This suggests that stem temperature is 2.0 °C higher than ambient temperature, and that ambient temperature elucidates 95% of the variability in stem temperature during the growing season of 2007. It suggests that a higher stem temperature may be due to a relatively larger heat capacity for the stem than the atmosphere.

3.2. Temperature dependency of stem respiration

The responses from stem respirations by different aged black spruce trees to temperatures in air and stem are shown in Fig. 4a–b, and represent an exponential curve. This implies the temperature dependence of stem respiration (Lavigne, 1996; Lavigne and Ryan, 1997; Zha et al., 2004; Harris et al., 2008; Kim et al., 2014). Stem respiration in the younger black spruce tree depends strongly on temperatures in air and stem, relative to old trees. Mean stem respiration for temperatures in air and stem is between 7.2 cm and 9.8 cm black spruce trees. As previously described, the response from 14.5-cm black spruce stem respiration appears to blunt temperatures in air and stem relative to other thinner trees, indicating that a thicker stem black spruce tree has much higher heat capacity than others, and then has much slower response to temperatures in air and stem.

Growing season and monthly Q_{10} values and coefficients of determination (R^2) calculated using equations (2) and (3) are listed in Table 1. The pattern of Q_{10} values for the four trees tended to increase from stem temperature to air temperature, suggesting the response in stem respiration to air temperature is quite sensitive to stem temperature (Lavigne, 1996; Lavigne and Ryan, 1997; Bolstad et al., 2004; Zha et al., 2004; Harris et al., 2008). Q_{10} values for temperatures in air and stem during the growing season ranged from 2.04 to 2.76, compared to 1.2–3.5 in the *Picea*, *Populus*, and *Pinus* species for air and stem temperature during growing seasons (Lavigne, 1996; Lavigne and Ryan, 1997; Bolstad et al., 2004; Zha et al., 2004; Harris et al., 2008).

Fig. 5 shows fifteen-day moving Q_{10} values, determined for each of measured trees using equations (6) and (7) during the growing season.

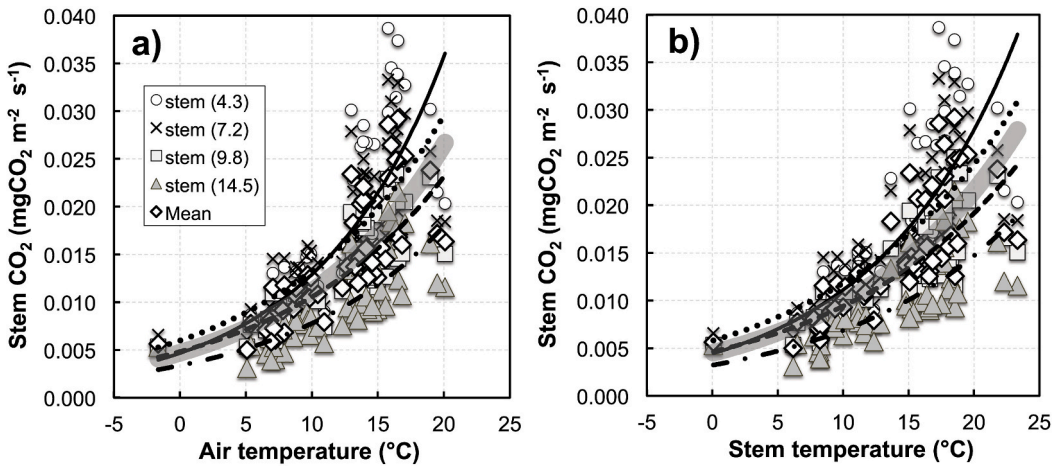

Fig. 4. Response from stem respiration of four different aged black spruce trees to temperatures of (a) air and (b) stem, indicating exponential relationships between stem respiration and temperatures in air and stem for 4.3 cm (solid curve), 7.2 cm (dotted), 9.8 cm (dashed), 14.5 cm (dash-dotted), and mean (thick grey curve) with 95% confidence level, respectively.

Table 1
Q_{10} values estimated by equation (2) and coefficients of determination (R^2) from the relationships between stem respirations and temperatures of air and stem in four differently aged black spruce trees in interior Alaska, during the growing season of 2007.

Stem	Total in growing season				July				August				September			
DBH [a]	AT [b]		ST [b]		AT		ST		AT		ST		AT		ST	
(cm)	Q_{10}	R^2	Q_{10}	R^2	Q_{10}	R^2	Q_{10}	R^2	Q_{10}	R^2	Q_{10}	R^2	Q_{10}	R^2	Q_{10}	R^2
4.3	2.76	0.71	2.51	0.71	2.15	0.78	2.13	0.83	2.16	0.66	2.19	0.72	1.90	0.60	2.08	0.74
7.2	2.22	0.65	2.05	0.65	2.22	0.84	2.17	0.87	2.28	0.77	2.26	0.79	2.12	0.69	2.28	0.78
9.8	2.19	0.70	2.04	0.70	1.79	0.67	1.80	0.75	1.89	0.71	1.91	0.76	1.64	0.52	1.78	0.67
14.5	2.31	0.64	2.14	0.65	2.01	0.82	1.93	0.80	2.06	0.73	2.03	0.73	1.94	0.52	2.05	0.57
Average	2.37	0.69	2.19	0.69	2.04	0.78	2.01	0.81	2.10	0.72	2.10	0.75	1.90	0.58	2.05	0.69

[a] DBH is the diamtere at breast height that stem chamber is mounted on the surface.

[b] AT and ST denote air and stem temperatures.

The thicker grey lines represent the mean and its 95% confidence level for temperatures in air and stem (Fig. 5a and b), respectively. During the growing season, mean Q_{10} estimated using air temperature was 2.49 for 4.3 cm, 2.44 for 7.2 cm, 2.46 for 9.8 cm, 2.46 for 14.5 cm, and 2.41 as mean for the four trees. Mean Q_{10} estimated using stem temperature was 2.63 for 4.3 cm, 2.68 for 7.2 cm, 2.67 for 9.8 cm, 2.60 for 14.5 cm, and 2.65 for mean of four trees. For Q_{10} determined using air temperature records (Fig. 5a), values generally fall from near 3.5 early in the monitoring period to roughly 1.5, and show a similar trend across the four trees. Fig. 5b shows fifteen-day moving Q_{10} values, determined using stem temperature and showing greater scattering, higher than those determined by air temperature.

Relationships between mean stem respiration (SR) and temperatures in air and stem were $SR = 0.0047 \times exp\ (0.0865 \times AT)$, $(R^2 = 0.69; Q_{10} = 2.36)$, and $SR = 0.0045 \times exp\ (0.0782 \times ST)$, $(R^2 = 0.69; Q_{10} = 2.19)$, respectively, suggesting temperature elucidates 69% (64–71%) and 69% (65–71%) of the variability in growing-season stem respiration, respectively, as listed in Table 1. This implies the temperature sensitivity of stem respiration (Lavigne, 1996; Lavigne and Ryan, 1997; Zha et al., 2004; Harris et al., 2008; Kim et al., 2014). Furthermore, temperature in July accounts for 78 and 81% in air and stem of the variability July stem respiration, respectively. This demonstrates the temperature dependency of July stem respiration is much higher than stem respirations in August and September, as shown in Fig. 5.

3.3. Simulated stem respiration based on air temperature

We further estimated simulated respirations (R_i), normalized to an air temperature of 10 °C (R_{10}), as well as Q_{10} values using equations 4 and 5 for mean stem respiration of the four trees. The relationship between simulated (SSR) and mean observed stem respiration (OSR) for the four trees denoted a positively linear relationship: $SSR = 0.89 \times OSR + 0.003$ $(R^2 = 0.87; p < 0.001)$, based on a one-way ANOVA at a 95% confidence level (Fig. 6). Simulated stem respiration (SSR) elucidated 87% of the variability in observed stem respiration (OSR) for each tree. Zha et al. (2004) reported the coefficient of determination (R^2) between SSR and OSR was 0.75–0.83 for three Scots pines.

Stem respiration was calculated as area (m^2) of stem surface covered by the chamber, and scaled for ground-level surface area of observed trees, allowing mean height, DBH, and total number of black spruce within a 60-m × 60-m plot. Nevertheless, this study could not measure branch respiration, due to the different sizes of branches and the existence of live/dead branches relative to stem—with stems even 7.8-times higher in weight than branch and foliage. Furthermore, this study assumed that the outer surface of each black spruce was a long conic shape. Table 2 lists mean simulated stem respiration on a ground level of four black spruce trees within a 60-m × 60-m plot during spring (DOY (day of year) 121–151), summer (DOY 161–241), fall (DOY 251–291), and winter (DOY 1–111 and DOY 301–361), at an interval of ten days.

Ueyama et al. (2014) reported that carbon exchange rates (i.e., GPP, NEE, and Re) estimated by eddy covariance tower method were determined in the same black spruce forest of interior Alaska. The stand-level

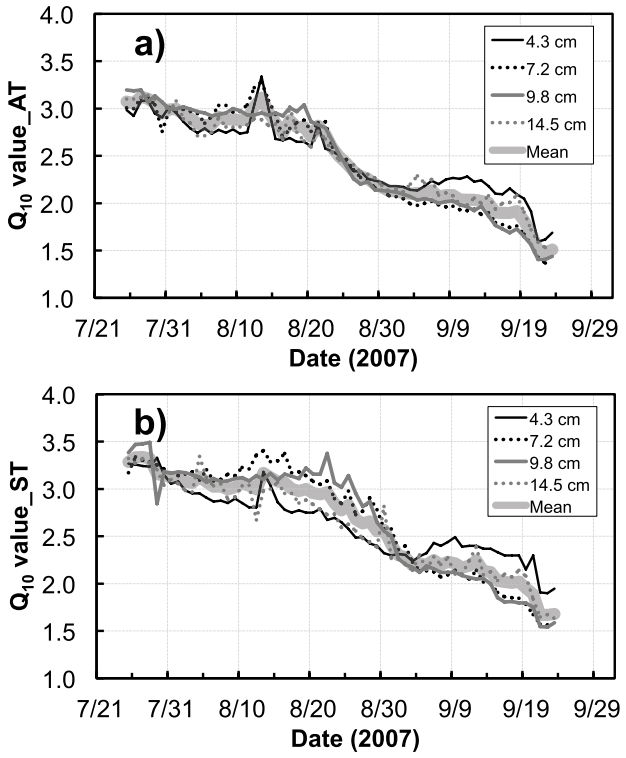

Fig. 5. Temporal variations in Q_{10} values using equations (6) and (7) for (a) air temperature and (b) stem temperature. Thick grey lines denote mean and its 95% confidence level, indicating that Q_{10} values tend to decrease with time.

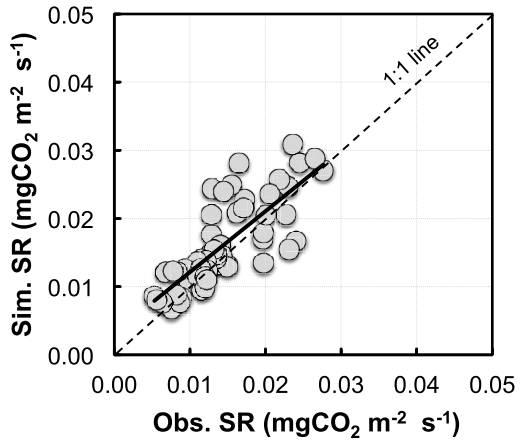

Fig. 6. Relationship between simulated stem respiration (SSR) and observed stem respiration (OSR), with normalized air temperature of 10 °C, showing equation SSR = 0.89 × SSR + 0.003 (R^2 = 0.87). Dashed line denotes a 1:1 line.

annual stem respiration simulated by Q_{10} value based on air temperature is 73.9 g CO_2 m^{-2}, corresponding to 5.0% of the annual ecosystem respiration (Re) estimated by eddy covariance tower in 2007. Also, seasonal stand-level mean simulated stem respiration (SSR) contributed 4.4, 3.8, 3.7, and 5.5% of ecosystem respiration (Re) as measured by eddy covariance during the spring, summer, fall, and winter seasons, respectively (Table 2). The contribution from simulated stem respiration to ecosystem respiration (Re), estimated by eddy covariance tower observation, ranged from 1.1 to 12.8%, denoting higher winter/spring contributions and lower summer/fall contributions to ecosystem respiration (Ryan and Waring, 1992; Livigne, 1996; Lavigne and Ryan, 1997; Vose and Ryan, 2002). The response from stand-level simulated stem

Table 2
Contribution (%) of simulated stem respiration estimated by equation (5) toward ecosystem respiration (Re), estimated by eddy covariance tower in black spruce forest in interior Alaska, during 2007.

DOY	Sim. stem respiration (gCO_2 m^{-2} d^{-1})	Re	Contribution (%)
1	0.009	0.072	12.6
11	0.023	0.147	15.8
21	0.029	0.338	8.6
31	0.022	0.341	6.5
41	0.021	0.344	6.0
51	0.009	0.645	1.3
61	0.013	0.653	2.0
71	0.020	0.660	3.1
81	0.026	0.722	3.6
91	0.095	1.541	6.2
101	0.110	1.250	8.8
111	0.158	2.401	6.6
121 [a]	0.182	3.137	5.8
131 [a]	0.215	3.869	5.6
141 [a]	0.322	5.571	5.8
151 [a]	0.335	6.886	4.9
161	0.373	8.724	4.3
171	0.403	12.584	3.2
181	0.466	13.504	3.5
191	0.390	12.185	3.2
201	0.567	11.221	5.1
211	0.460	9.011	5.1
221	0.424	11.079	3.8
231	0.307	10.251	3.0
241	0.248	9.270	2.7
251 [b]	0.210	6.949	3.0
261 [b]	0.138	4.031	3.4
271 [b]	0.109	2.163	5.0
281 [b]	0.063	2.121	3.0
291 [b]	0.049	1.229	4.0
301	0.047	1.086	4.4
311	0.034	1.087	3.2
321	0.052	0.762	6.8
331	0.026	0.658	4.0
341	0.037	0.745	5.0
351	0.014	0.801	1.7
361	0.017	0.333	5.1
Average	0.163	4.01	5.0
Stdev	0.167	4.38	2.9

[a] and [b] denote spring and fall of 2007, respectively.

respiration (SSR) to GPP and Re from eddy covariance tower represented a linear relationship of $GPP = 46.6 \times SSR - 0.41$ ($R^2 = 0.89$) and $Re = 30.8 \times SSR - 0.068$ ($R^2 = 0.89$), respectively, indicating that stem respiration (SSR) accounts for 89% of the variability in GPP and Re in the black spruce forest of interior Alaska (not shown). Zha et al. (2004) noted that stem respiration (SSR) accounts for 65–71% of the variability of GPP in Scots pine trees in a boreal forest.

Tang et al. (2008) noted that stem respiration contributed to 13% of ecosystem respiration, while soil respiration accounted for 72% of ecosystem respiration in the old-growth hardwood forest of Ottawa National Forest in Michigan, USA. In the central Siberian forest, Shibistova et al. (2002) estimated the respirations of soil, stem, and foliar were attributable to 61, 21, and 18%, respectively, of the annual respiratory emission of a Scots pine (*Pinus sylvestris*) stand. Bolstad et al. (2004) further noted that stem respiration explained 20% and 11% of total respiration (i.e., leaf and stem) of northern hardwood and mature aspen, respectively. Soil respiration contributed 75 and 81% of total respiration in northern hardwood and mature aspen (Bolstad et al., 2004). Stem respiration was estimated to comprise from 9% in a 50-year-old stand of Scot pine (Zha et al., 2004) to as much as 13% (Ryan and Waring, 1992) in a 245-year-old stand of lodgepole pine, for which the contribution was within the ranges of our winter results

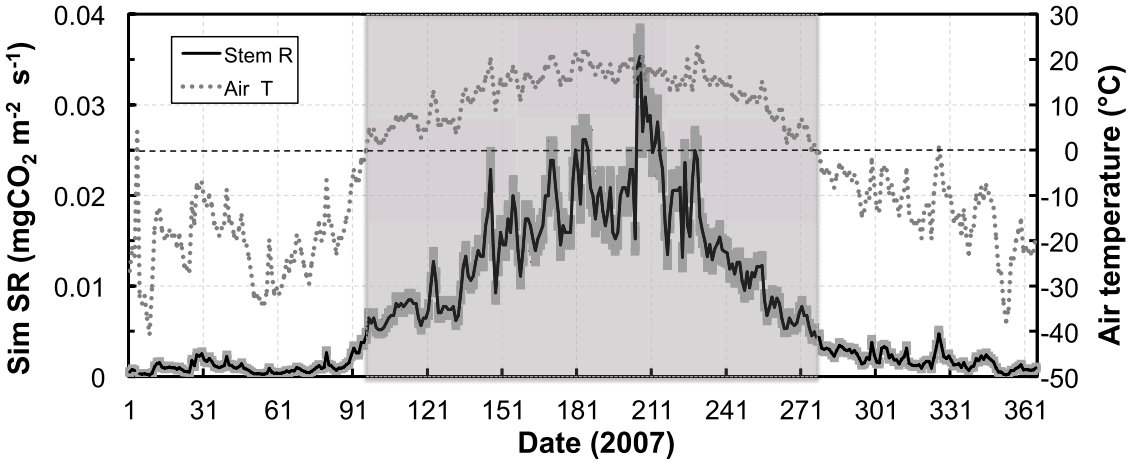

Fig. 7. Temporal variations in simulated stem respiration (solid line) with errors (grey) and temperatures of air (grey dotted line). Grey shade box denotes growing season stem respiration above zero from April 7 to October 10, 2007.

(Table 2). Although this study could not conduct winter measurements of stem respiration for four differently aged black spruce trees, we can estimate simulated stem respiration based on air temperature and observed growing season stem respiration.

In Fig. 7, annual simulated stem respiration is divided into growing (shaded) and non-growing stem respirations, based on the air temperature of zero. Growing season for the black spruce tree is from April 7 to October 1 (178-day) for above-zero temperatures, while the non-growing season is January 1 to April 6 and October 2 to December 31 (187-day). Summed growing and non-growing stem respirations were 1.23 and 0.13 kg CO_2 m^{-2}, respectively. Non-growing stem respiration contributes 9.5% of annual simulated stem respiration.

4. Summary and conclusions

Temporal variations in stem respiration for these four differently aged black spruce trees were modulated by changes in air and stem temperatures, which are key in determining and simulating stem respiration; this response from stem respiration to temperature is likely to depend on the observed diameter of black spruce during the growing season of 2007. Simulated stem respiration, Q_{10} adjusted and normalized to an air temperature of 10 °C (R_{10}), accounted for 87% of measured stem respiration averaged the four trees. The research findings demonstrate that stem respiration is a significant component for scaling up an ecosystem carbon budget and should not overlooked. However, additional study is needed to determine year-round stem respiration with FD (forced diffusion) CO_2 chamber system (Risk et al., 2011; Kim et al., 2016). Additional work is also required to investigate the relationships between stem respiration and soil moisture at each tree and between stem respiration and the radial growth rate of black spruce, for the quantitative evaluation of the stem respiration-precipitation and other climate-related trends during the growing season.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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