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Vertical gradients and seasonal variations in the stem CO_2 efflux of *Larix principis-rupprechtii* Mayr

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ABSTRACT

Stem CO_2 efflux (E_S) plays an essential role in the carbon balance of forest ecosystems. Therefore, it is necessary to study the vertical and seasonal variations in E_S in forests with different ages, especially in response to factors associated with temperature, nutrients and wood structure. In this study, we investigated E_S and its association with temperature factors using a carbon flux system (Li-8100A) at monthly intervals during the growing season (May to September) and the non-growing season (October) from 2013 to 2015. In addition, we collected data on nutrients and wood structure in August 2016 from 16- (young), 25- (immature), and 41-year-old (mature) *Larix principis-rupprechtii* Mayr stands in North China. Our analysis showed that the E_S values at stem positions near the crown and the root system were generally higher than those in the middle and that the minimum E_S values in July occurred at 2.0 m (3.61 $\mu mol\ m^{-2}\ s^{-1}$), 3.0 m (2.42 $\mu mol\ m^{-2}\ s^{-1}$), and 5.0 m (4.03 $\mu mol\ m^{-2}\ s^{-1}$) in the young, immature, and mature forests, respectively. Air temperature and wood temperature influenced the vertical variation in E_S, as did stem nitrogen concentration and sapwood width. Compared to the method that uses the vertical E_S gradient to determine tree-scale CO_2 effluxes for 16-, 25- and 41-year-old *L. principis-rupprechtii* forests, the method that uses the E_S value at the 1.3-m stem position underestimated the CO_2 effluxes by 5%, 6%, and 24%, respectively. The E_S and Q_{10} models for each stem position for the three forest ages in this study can be used to accurately estimate tree-scale CO_2 effluxes. These results not only clarified the relationships between the vertical variation in E_S and temperature, nutrient content and wood structure, but also revealed the likely response mechanisms of E_S to these factors. Methodologically, incorporating the vertical variation in E_S and the associated drivers into conventional models would improve the accuracy of annual E_S estimates.

1. Introduction

The carbon balance of forests has received increasing attention in recent decades, and tree respiration is widely recognized to play an essential role in the carbon balance of forest ecosystems (Carey et al., 1997; Damesin et al., 2002; Sprugel et al., 1995; Reinmann and Templer, 2016). A substantial part of the carbon that is assimilated during photosynthesis (approximately 50–70%) is used for respiration in plant tissues and is released back to the atmosphere (Hagihara and Hozumi, 1983; Sprugel and Benecke, 1991; Ryan et al., 1994; DeLucia et al., 2007; Litton et al., 2007). Stem CO_2 efflux (i.e., stem respiration) accounts for 10–42% of the aboveground total carbon budget in various types of forest (Waring and Schlesinger, 1985; Carey et al., 1996; Landsberg and Gower, 1997; Ryan et al., 1997; Araki et al., 2010). Stems emit carbon dioxide (CO_2), and the stem CO_2 efflux (E_S) can rival the emissions per unit area from leaves or the soil surface and, when summed over a forest stand, can comprise 14–48% of the total ecosystem CO_2 efflux (Ryan, 1991; Ryan et al., 1996; Vose and Ryan, 2002; Chambers et al., 2004). Therefore, with the emergence of global warming, there is increasing interest in studying E_S variation and estimating the annual E_S at the whole tree level (Zha et al., 2004; Teskey et al., 2008; Araki et al., 2010).

Some studies have suggested that ignoring vertical variation in E_S may cause considerable error in tree-scale estimates of E_S (Araki et al., 2010; Stockfors, 2000; Tarvainen et al., 2014), but few studies have sufficiently accounted for the vertical variations of E_S in trees of different ages and sizes to represent the whole stem in E_S calculations (Ryan et al., 1996; Ceschia et al., 2002; Tarvainen et al., 2014). Few

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long-term studies have continuously measured E_S at several stem positions (Ryan et al., 1996; Ceschia et al., 2002; Ryan et al., 2009); therefore, it is important to clarify the vertical variations in E_S using continuous long-term monitoring in forests of different ages to precisely evaluate the annual release of CO_2 from stem surfaces at different stem positions.

Respiration rates are affected by climatic factors (Ryan et al., 1995; Jiang et al., 2003; Williams et al., 2014; Lombardozzi et al., 2015), especially temperature (Stockfors and Linder, 1998; Ceschia et al., 2002; Kim et al., 2007; Acosta et al., 2007; Gruber et al., 2009). Some studies have shown a correlation between variation in E_S and air temperature and have suggested that there is no significant difference between air temperature (T_a) and wood temperature (T_w) (Ryan, 1990, Ryan et al., 1995; Ceschia et al., 2002); however, T_w is expected to be more closely related to E_S (Stockfors, 2000). Thus, reliable estimates of forest carbon budgets require careful comparison of the effects of these temperature factors on vertical variation in E_S values of trees and clarification of the most appropriate temperature model to explain this vertical variation in E_S.

Temperature affects E_S by influencing cellular physiological activity (Reich et al., 2016; Sperling et al., 2017). Some studies have suggested that respiration in living cells mostly varies with enzyme content (Ryan, 1991), which is closely related to nutrient elements (Ryan et al., 1997; Yan et al., 2016), especially nitrogen concentrations (Maier et al., 1998; Maier, 2001; Ceschia et al., 2002). The concentrations of nutrient elements in woody tissues are correlated with E_S in several forest tree species (Kawahara et al., 1976; Reich et al., 1998; Gunderson et al., 2000; Vose and Ryan, 2002; Burton et al., 2002) and have been proposed to be a scaling variable for E_S (Sprugel et al., 1995). Therefore, a comprehensive analysis of the effects of nutrient elements on E_S in forest stands of different ages, including identifying the most important nutrient elements and establishing an estimation model, will play an important role in the accurate estimation of forest carbon emissions.

Recent studies have revealed that stem structures (such as the sapwood, cambium and bark) that have high resistance to radial CO_2 diffusion, and contain living cells that release CO_2, can influence E_S (Steppe et al., 2007; Jesús et al., 2015). Because of this high resistance in the xylem, cambium and bark, a considerable portion of CO_2 produced by stem cellular respiration can be retained in the xylem sap and move upward via the transpiration stream (Bowman et al., 2005; Levy et al., 1999; McGuire et al., 2007; McGuire and Teskey, 2004; Teskey and McGuire, 2002, 2005). Likewise, a fraction of respired CO_2 originating from the lower section of the stem can dissolve into the xylem sap and be transported to sites where efflux measurements are conducted (Aubrey and Teskey, 2009; Bloemen et al., 2013, 2014). Therefore, understanding how wood structures affect E_S may improve our understanding of the mechanisms contributing to vertical variation in E_S.

We employed the Li-8100 A respiration system to investigate vertical variation in E_S for 16- (young), 25- (immature), and 41-year-old (mature) *Larix principis-rupprechtii* Mayr forests at monthly intervals during the growing season (May to September) and the non-growing season (October) from 2013 to 2015 in North China.The overall motivation for this study is to facilitate the construction of an accurate model to estimate forest carbon emissions. We evaluated the effects on E_S of temperature factors (T_a and T_w, both in °C), stem nutrient concentrations (nitrogen in (mg N g^{-1} DM, abbreviated C_N;), phosphorus (mg P g^{-1} DM, abbreviated C_P), and potassium (mg K g^{-1} DM, abbreviated C_K)), and wood structures (bark thickness (cm, abbreviated BT), sapwood width (cm, abbreviated SW), heartwood radius (cm, abbreviated HR), and sapwood growth rate (cm^2 $year^{-1}$, abbreviated SR)). This study was conducted with five objectives: (1) to clarify the seasonal variation in E_S at several stem positions in forests of three ages; (2) to determine the primary factors influencing E_S and construct a model relating these factors to E_S for the three forest ages; (3) to establish a model of E_S for each stem position and calculate the sensitivity of E_S to air temperature; (4) to evaluate the degree of error in the estimations of annual tree-scale CO_2 efflux when vertical variations in E_S in the three forest ages are not considered; and (5) to perform a preliminary investigation of the regularity and mechanisms by which E_S responds to temperature, nutrient elements and wood structures. The results of this study help to identify the mechanisms controlling the seasonal and vertical variations in E_S.

2. Materials and methods

2.1. Site description

This study was conducted in L. *principis-rupprechtii* forests that were 16, 25, and 41 years old in 2013 in the Saihanba National Forest Park (SNFP) of Weichang Manchu and Mongolian Autonomous County in Hebei Province (42°02′-42°36′ N; 116°51′-117°39′ E), Northern China. This area features a semi-arid monsoon climate and is located in a cool temperate zone. The basic information is as follows: elevation, 1600–1800 m; annual average temperature, -1.5 °C; maximum temperature, 29.7 °C; minimum temperature, -38.7 °C; active accumulated temperature (≥ 10 °C), 1663.5 °C; and average annual rainfall, 433 mm. The precipitation in June and August accounts for 55% of the total annual precipitation (Fig. 1). The soil is composed mainly of grey forest soilpredominantly consisting of sand (Xi, 1994). Based on 0–40 cm depth soil,the soil bulk density is 1.18–1.27 g cm^{-3}, the soil pH (soil: water, 1:2.5) is 6.3 ± 0.2, and the C: N ratio is 8.9 ± 0.3 (Ma et al., 2014; Liu et al., 2013). The soil parent materials are eluvium, saprolite, and alluvium. The thickness of the organic surface horizon is approximately 3–8 cm in all stands (Wang et al., 2014). In total, 77.1% of the total plantation area in the SNFP is *L. principis-rupprechtii*, but the SNFP also containsChinese pine (*Pinus tabulaeformis* Carr.), Scots pine (*Pinus sylvestris* var. *mongolica* Litv.), spruce (*Picea asperata* Mast.), and birch (*Betula platyphylla* Buk.).*L. principis-rupprechtii* is the dominant species in the coniferous forest belt of North China (Yao et al., 2013).

2.2. Stem CO_2 efflux measurements

L. principis-rupprechtii stand volumes reach their peak at 39 years in the SNFP (Zhao et al., 2015); thus, trees in the SNFP are generally harvested after 40 or more years of growth. New seedlings are manually replanted. Areas with *L. principis-rupprechtii* plantations older than 40 years are very rare in the SNFP. In our study, the 30 × 30 m experimental site included artificial larch forests with ages of 16, 25, and 41 years (young, immature, and mature, respectively). This study involved a total of five *L. principis-rupprechtii* stands in each forest age with

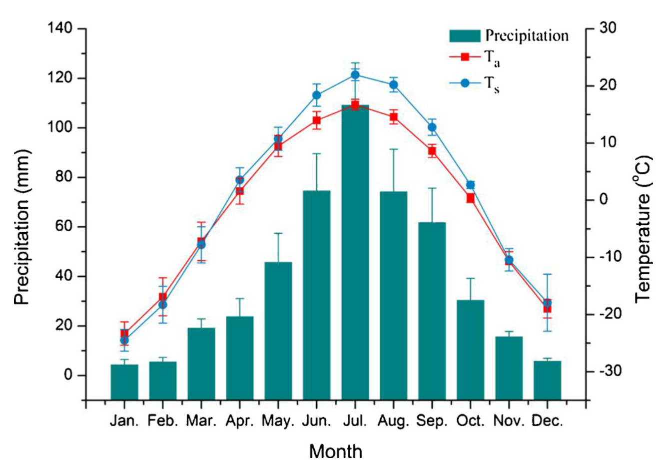

Fig. 1. Monthlymean precipitation, air temperature (T_a) and soil temperature (T_s) in the Saihanba National Forest Park (SNFP) (1996–2013). Error bars indicate the standard error, n = 9 (Zhao et al., 2018).