



Conversion of primary mixed forest into secondary broadleaved forest and coniferous plantations: Effects on temporal dynamics of soil CO₂ efflux

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ARTICLE INFO

Keywords:

Forest conversion
Temporal variability
Heterotrophic respiration
Autotrophic respiration
Soil temperature

ABSTRACT

Soil CO₂ efflux varies significantly in time and space in terrestrial ecosystems, obtaining a detailed understanding of what controls the dynamics of soil respiration (SR) can improve the estimation accuracy of forest carbon budgets. We examined the effects of forest conversion (from primary forest to both secondary forest and coniferous plantations) on the temporal dynamics of SR and its components (heterotrophic = R_H , and autotrophic = R_A), at both seasonal and inter-annual time scales within four adjacent forest stands in north-eastern China. Trenching method was used to partition R_H and R_A . The results showed that R_H was the primary contributor to the overall magnitude and variability of SR, which showed similar seasonal and inter-annual variation, while R_A displayed higher temporal variation compared to SR and R_H . Generally, the between-year seasonal variation of SR and R_H varied significantly in both secondary forest and plantations. The secondary forest exhibited a relatively higher seasonal change in R_A compared to that in primary forest and coniferous plantations, while there was no significant disparity in the seasonal and inter-annual variation of SR and R_H among forest stands. Soil temperature was the primary factor driving the temporal dynamics of R_H and accounted for 63–91% and 22–64% of seasonal and inter-annual variations, respectively. However, R_A was less controlled by soil temperature. This study implies that forest conversion magnifies the responses of R_H to the minor variations in the between-year seasonal patterns of soil temperature and increases the seasonal variability of R_A .

1. Introduction

Land-use change plays an important role in the global carbon (C) cycle, and investigating its effects on terrestrial ecosystem C dynamics is critical to understanding its role in future climate change (Raich and Tufekciogul, 2000). Forest conversion can result in a major contribution to greenhouse gas emissions by causing changes in tree species composition, stand structure and soil properties (Lorenz and Lal, 2010; Shi et al., 2015). Soil respiration (SR) is the largest C flux from ecosystems to the atmosphere and is a key component for estimating forest C budgets (Luo et al., 2001; Rey et al., 2002). SR is composed of autotrophic (R_A , root and associated mycorrhizae) and heterotrophic (R_H , soil microbes and fauna) respiration. As resulting from the different organisms, C sources and processes driving these two source components, SR vary substantially across space and time (Kuzakov, 2006; Moyes and Bowling, 2012; Chen et al., 2014a; Han et al., 2014). Consequently, quantifying the temporal dynamics of SR and its components

and identifying the corresponding controlling factors are necessary when assessing the potential influences of forest management and climate change (Raich and Tufekciogul, 2000; Lorenz and Lal, 2010).

Overall, despite numerous in situ observations of SR over the last two decades, there is still a limited understanding of the key abiotic and biotic factors that control the temporal and spatial variability of SR (Chen et al., 2014b). Various climatic conditions have been found to control the seasonal variation of SR, of which the most influential factors are the soil temperature (T_s) and soil moisture (W_s) (Wang et al., 2006). A temperature-dependent exponential correlation against the soil CO₂ efflux is commonly accepted (Lloyd and Taylor, 1994). However, SR often increases with W_s from the wilting point value until it reaches the threshold of the volumetric water content, after which SR is negatively linked to W_s (Wang et al., 2006; Cartwright and Hui, 2015). T_s , which could also be confounded by W_s , is usually the largest driving factor for the seasonality of SR in boreal and temperate forests (Laganière et al., 2012; Shi et al., 2015). In tropical forests, however,

Abbreviations: SR, soil respiration; R_H , heterotrophic respiration; R_A , autotrophic respiration; T_s , soil temperature; W_s , soil moisture; MBKP, mixed broadleaved-Korean pine forest; BP, secondary birch forest; KP, Korean pine plantation; LG, Dahurian larch plantation

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<https://doi.org/10.1016/j.catena.2017.12.004>

Received 18 March 2017; Received in revised form 27 November 2017; Accepted 5 December 2017
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seasonal changes in SR are significantly linked to W_s due to the low seasonality of temperature (Ohashi et al., 2008). At smaller timescales, such as diurnal, various environmental factors, such as T_s (Hanpattanakit et al., 2015), photosynthesis (Savage et al., 2013) and rain pulses (Daly et al., 2008), have been found to regulate the diel variation of SR in different forest ecosystems. At longer timescales, such as inter-annual or decadal, weather and climatic perturbations (e.g., annual precipitation and drought events), natural recovery and disturbance as well as management practices (e.g., fire and thinning), would alter the inter-annual dynamics of the soil CO₂ efflux (Moyes and Bowling, 2012; Lopez-Serrano et al., 2016). Compared to SR, there are few reports concerning the temporal variations of R_A and R_H at long timescales (such as inter-annual or longer) (Hanpattanakit et al., 2015). For forest ecosystems, a wide range (10–90%) exists, and mean values of 45–50% for the contribution of R_A to SR, have been reported (Hanson et al., 2000). The sensitivity of SR to T_s and W_s has been found to depend on the relative contributions of R_A and R_H to SR (Hanpattanakit et al., 2015). Moreover, photosynthesis is another important factor that determines the magnitude and temporal variation of R_A (Savage et al., 2013), and which may lead to the insensitivity of SR to T_s or to an unrealistic temperature sensitivity of SR. The conversion from primary forest to secondary forest or plantations brings about changes in these environmental and soil factors, i.e., T_s , W_s , total radiation and litterfall, which may alter the temporal dynamics of SR and its components (Shi et al., 2015; Lopez-Serrano et al., 2016). Currently, however, the effect of forest conversion on the temporal dynamics of SR across multiple timescales has not been thoroughly examined, especially for its two dominant components, and the corresponding driving factors may vary at different timescales (Hanpattanakit et al., 2015). The lack of such knowledge limits our understanding of the effects of forest management on soil C dynamics.

A variety of methods have been used to separate soil CO₂ efflux into R_A and R_H (Hanson et al., 2000; Kuzyakov, 2006; Shi et al., 2015), including component integration, root exclusion and isotopic approaches. However, it is still challenging to measure root respiration under field conditions. The trenching method is probably the most common method used in the field. Although the results of component partition could be complicated by the inanition of the rhizosphere and disturbance of microbial activity (Bowden et al., 1993; Jiang et al., 2005), the trenching method is easy to conduct under experimental conditions and is suitable for maintaining most field conditions. Furthermore, it can provide realistic estimates of R_H and R_A when methodological problems (such as water regime, microbe disturbance, decomposition of dying roots and interruption of underground substrate supply) are adequately addressed (Díaz-Pinés et al., 2010). On the other

hand, because the vitality of mature trees is vulnerable to root trenching, trenching is the most suitable method for separating R_A and R_H in long-term studies (Díaz-Pinés et al., 2010). Hence, the trenching method would be an effective root-exclusion approach to partition the source components of SR in forest ecosystems (Zeng et al., 2016; Noh et al., 2017).

The zonal climax vegetation in northeast China primarily comprises mixed broadleaved-Korean pine (*Pinus koraiensis*) forests. Over the past few decades, a large tract of primary forest has been transformed into secondary broadleaved forest and coniferous plantations after harvest, as a result of the development of intensive timber exploitation. The Heilongjiang Liangshui National Nature Reserve (47°10'50" N, 128°53'20" E) contains a variety of forest stands with different management regimes that are within a restricted geographic region and have similar air temperatures, precipitation and soil types. Therefore, it provides a good opportunity to identify the temporal dynamics of SR and its components in different forest stands, with respect to forest conversion. In the present study, we conducted measurements of SR, R_H and R_A using the trenching method in four distinct forest stands (from primary forest to secondary forest and plantation). Our primary objectives were to (1) assess the temporal variations in SR, R_H and R_A across the four forest stands, (2) determine the environmental drivers of seasonal and inter-annual patterns of the component parts of SR, and (3) determine the effects of forest conversion on the temporal dynamics of SR and its components.

2. Materials and methods

2.1. Site description and experimental design

This study was conducted at the Heilongjiang Liangshui National Nature Reserve (47°10'50" N, 128°53'20" E) in north-eastern China. This region lies on the eastern part of Eurasia and has a typical hilly landscape. The climate is continental monsoon. The mean annual temperature is $-0.3\text{ }^{\circ}\text{C}$, and the mean annual precipitation is 676 mm. The growing season is relatively short, with 100–120 frost-free days. The soil is Humaquepts or Cryoboralfs, based on the American Soil Taxonomy (Soil Survey Staff, 2014). We selected four forest stands with different land-use histories in this region, including a primary mixed broadleaved-Korean pine forest (MBKP), a secondary birch (*Betula platyphylla*) forest (BP), a Korean pine plantation (KP) and a Dahurian larch (*Larix gmelinii*) plantation (LG). These four forest stands are similar in topography and microclimate. The site and soil characteristics of the four forest stands have been described in Table 1.

In October 2009, at each forest stand, three 20 m × 30 m plots were

Table 1
Soil properties (depth: 0–10 cm) and forest characteristics across the four forest stands.

Properties	MBKP	BP	KP	LG
Soil properties				
Bulk density (g cm^{-3})	0.63 ± 0.17	0.53 ± 0.03	0.59 ± 0.01	0.63 ± 0.01
pH	5.9 ± 0.1	4.8 ± 0.1	5.4 ± 0.1	5.4 ± 0.1
Organic carbon (g kg^{-1})	47.8 ± 6.6	66.8 ± 5.6	48.6 ± 3	66.9 ± 9.5
Total N (g kg^{-1})	7.0 ± 0.9	9.9 ± 1.5	6.2 ± 0.3	7.1 ± 0.3
Stand characteristics				
Tree density (trees ha^{-1})	3406 ± 245	2475 ± 316	2072 ± 116	2233 ± 127
Basal area ($\text{m}^2 \text{ha}^{-1}$)	33.0 ± 0.9	23.2 ± 2.2	41.6 ± 3.6	32.1 ± 1.2
Mean DBH (cm)	11.2 ± 0.6	8.4 ± 1.8	16.0 ± 1.1	8.8 ± 0.5
Primary species composition	<i>Pinus koraiensis</i> , <i>Betula costata</i> , <i>Tilia amurensis</i> , <i>Acer ukurunduense</i> , <i>Abies nephrolepis</i> , <i>Ulmus laciniata</i> , <i>Acer tegmentosum</i>	<i>Betula platyphylla</i> , <i>Larix gmelinii</i> , <i>Picea koraiensis</i> , <i>Ulmus laciniata</i> , <i>Alnus sibirica</i>	<i>Pinus koraiensis</i>	<i>Larix gmelinii</i>

Stands are the mixed broadleaved-Korean pine forest (MBKP), the secondary birch forest (BP), the Korean pine plantation (KP), and the Dahurian larch plantation (LG). Means $\pm$ SE.

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