

Photosynthate supply drives soil respiration of *Fraxinus mandshurica* seedlings in northeastern China: evidences from a shading and nitrogen addition experiment

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Received: 12 March 2015 / Accepted: 22 June 2015 / Published online: 6 May 2016
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Abstract Improved understanding of the link between photosynthesis and below-ground processes is needed to better understand ecosystem carbon (C) cycling and its feedback to climate change. We conducted a short-term shading and nitrogen (N) addition experiment from June to September 2013 to investigate the effect of photosynthate supply by Manchurian Ash (*Fraxinus mandshurica*) seedlings on soil respiration (SR). Shading significantly reduced SR in early and middle growing season, but not in late growing season, leading to a decrease in mean SR by 24 % in N-unfertilized treatments. N addition increased mean SR by 42 % in un-shaded treatment. The stimulation of SR was largely attributed to accelerated autotrophic respiration by increasing photosynthesis, leaf area index and belowground biomass. Shading reduced mean SR by 32 % in N addition treatment. The strengthened shading effect on SR resulted from N addition was because of more photosynthates supply at low soil temperature. Our findings highlight the predominance of photosynthates supply in regulating the responses of C cycling to global change.

Keywords Autotrophic respiration · Carbon · Fertilization · Shading · Substrate supply

Introduction

As the second largest engine of carbon flux after photosynthesis in the terrestrial carbon cycle (Raich and Schlesinger 1992), soil respiration (SR) has drawn widespread attention as a result of its vulnerability to climate change (Luo et al. 2001; Luo and Zhou 2006; Davidson and Janssens 2006). SR is comprised of autotrophic respiration (R_A) from plant roots and rhizosphere microbes, and heterotrophic respiration (R_H) from decomposition of dead organic matter in soil (Hanson et al. 2000). An increasing body of evidence has demonstrated the important role of photosynthesis in controlling SR by supplying photosynthates for R_A (Ekblad and Högberg 2001; Moyano et al. 2008; Kuzyakov and Gavrichkova 2010; Subke et al. 2011). Tight linkage between SR and photosynthesis has been reported on various timescales (Tang et al. 2005; Bahn et al. 2008; Yan et al. 2011). Thus, any alteration in environmental factors affecting photosynthesis or availability of recent photosynthates is assumed to influence SR. Shading, or reducing the light involved in photosynthesis, has significantly reduced SR in grasslands (Craine et al. 1999; Wertin and Teskey 2008). However, the SR response to shading of trees or seedlings is not well documented.

Atmospheric nitrogen (N) deposition, one major component of climate change, has enormous impact on the global N cycle (Lamarque et al. 2005) and is predicted to increase in future (Erismann et al. 2011). However, large variations and inconsistencies in SR have been reported in response to the addition of N (Olsson et al. 2005; Mo et al. 2007; Allison et al. 2008). Because soil respiration arises

Project funding: This study was financially supported by the National Natural Science Foundation of China (41375119, 31400541) and the Key Laboratory of Forest and Soil Ecology (LFSE2013-11).

The online version is available at <http://www.springerlink.com>

Corresponding editor: Yu Lei

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from two main sources, the different responses of R_A and R_H might explain the reported conflicts in results. Responses of R_A and R_H to N addition are not consistent. Phillips and Fahey (2007) presented evidence that decreased SR was due to the reduction of R_H in fertilized forest soils, while Olsson et al. (2005) attributed it to a decrease in R_A . Addition of N influences photosynthate supply (Xu and Wan 2008; Gao et al. 2014). Thus the conflicting responses of SR after addition of N could derive from varying levels of photosynthate supply for R_A . This highlights the need for linking respiration to photosynthesis under N addition.

Fraxinus mandshurica is the dominant tree species in a temperate broad-leaved Korean Pine forest in northeast China. It is a fast-growing broad-leaved tree with relatively high photosynthetic activity (Wang et al. 2012). The aim of this study was to determine the impact of shading and N addition on soil respiration beneath *F. mandshurica* trees.

Materials and methods

The field experiment was conducted at the Research Station of Changbai Mountain Forest Ecosystem, Chinese Academy of Sciences (42°24'09"N, 128°05'45"E, and 738 m asl.). The site has a temperate continental climate, with mean annual temperature of 3.6 °C and mean annual precipitation of 695 mm.

The experiment was established in early May in 2013 as a complete randomized design with N addition (N) and shading (S) treatments. Sixteen pots were each planted with one *F. mandshurica* seedling (5-year-old, 1 m height) and were assigned to one of the following treatments (N = 4): control (CC), shading (CS), N addition (NC) and shading plus N addition (NS). In shading treatments, a single layer of black nylon cloth was hung 0.2 m above of the canopy for 3 days, reducing photosynthetic available radiation (PAR) by 95 %. Nitrogen was added as NH_4NO_3 in liquid form on 27 May and 2 July at 6.9 g m^{-2} per year and control pots received the same amount of water only. To measure heterotrophic respiration (R_H), seedlings in eight pots were removed on 1 May, then half of them were added the NH_4NO_3 solution and the others were added water only. Thus, autotrophic respiration (R_A) could roughly be determined by the difference in soil respiration measured in the planted and unplanted pots. Soil collars (11 cm in diameter and 5 cm in height) were inserted 2.5 cm into the soil in each pot about a week before the first measurement of SR and R_H . SR and R_H were measured on three sunny days at 2 h intervals from 6:00 to 20:00 in the early (8–10 June), middle (15, 17–18 July) and late (19–21 September) growing season using a LI-6400 portable photosynthesis system attached to a soil CO_2 efflux chamber (LI-6400, LI-

COR Inc.), which was accompanied by recordings of soil temperature at 10 cm depth (type 109, Campbell Scientific Inc., USA) and volumetric soil water content at 10 cm depth (TDR200, Spectrum, USA).

The maximum net photosynthetic rate (A_{max}) was recorded on sunny days of 6 June, 13 July and 15 September (8:00–11:00) by fitted light response curve of leaves according to Farquhar et al. (2001). Leaf area index (LAI) was measured at about 2-week intervals from 2 June to 21 September using a leaf area meter (LI-2000, Li-Cor). All seedlings were harvested on 23 September and divided into fine-root (diameter ≤ 2 mm), coarse-root (diameter > 2 mm), leaf and stem, and then oven-dried at 80 °C for 48 h, and then weighed to determine their dry biomass.

Data analyses were performed with SPSS 16.0 for Windows. Statistical significance was defined at the 95 % confidence level ($\alpha = 0.05$). Two-way ANOVA was performed to examine the effects of N addition and shading on soil respiration and its temperature sensitivity (Q_{10}). The main effects were significant ($P < 0.05$) and the interactive effect was not. The Q_{10} values were calculated according to the following equations (Boone et al. 1998):

$$y = \alpha e^{\beta T} \quad (1)$$

$$Q_{10} = e^{10\beta} \quad (2)$$

where, y is soil respiration, α and β are fitted constants, and T is soil temperature.

Results and discussion

Shading reduced SR by 35 % ($P < 0.01$), 24 % ($P < 0.05$) and 4 % ($P > 0.05$) in the early, middle and late growing season, respectively. This led to a decrease in the growing season mean SR by 24 % ($P < 0.05$) in unfertilized treatments (Fig. 1a). This reduction was lower than the 40 and 46 % decreases in SR within 2 and 4 days in grasslands, respectively (Craine et al. 1999; Wan and Luo 2003). The differences mainly derive from different vegetation types and stages of growing season. It is possible that the seasonal effect of shading on SR was due to the seasonality of photosynthesis (Wu et al. 2012) and photosynthates allocation (Meng et al. 2013).

There were significant exponential relationships between SR and soil temperature among treatments ($P < 0.001$) (Table 1). Shading had no significant effect on coefficient a (basal respiration) among treatments, while it decreased coefficient b . Consequently, Q_{10} values of SR were 13 % lower ($P > 0.05$) and 15 % lower ($P < 0.05$) in CS and NS treatments than in CC and NC treatments, respectively (Table 1). This implies that R_A should be more sensitive to soil temperature change than R_H , for R_A is

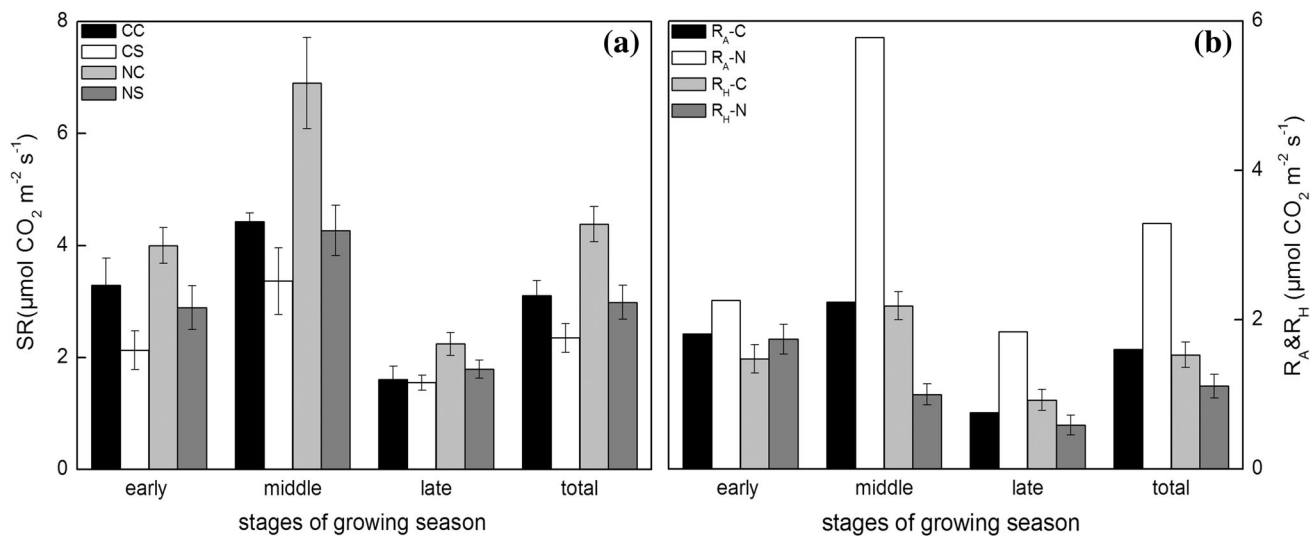


Fig. 1 Overall mean SR in control (CC), shading (CS), N addition (NC) and shading plus N addition (NS) treatments in different stages of growing season (a) and autotrophic respiration (R_A) and

heterotrophic respiration (R_H) at N-fertilized (N) and unfertilized (C) treatments in different stages of growing season (b). Error bars represent standard deviation (n = 4)

Table 1 Values of coefficients a and b of the Eq. ($R_S = ae^{bT}$), regression equations fitness index (R^2), sensitivity of soil respiration (SR), autotrophic respiration (R_A) and heterotrophic respiration (R_H) to soil temperature (Q_{10}) and P values among different treatments

CO ₂ fluxes	Treatments	Fitted a	Fitted b	R^2	Q_{10}	P
SR	CC	$0.4029 \pm 0.02c$	$0.0938 \pm 0.01a$	0.7388	$2.56 \pm 0.1a$	<0.001
	CS	$0.4559 \pm 0.04bc$	$0.0803 \pm 0.01ab$	0.6582	$2.24 \pm 0.2ab$	<0.001
	NC	$0.5492 \pm 0.1ab$	$0.0946 \pm 0.01a$	0.7381	$2.58 \pm 0.3a$	<0.001
	NS	$0.6032 \pm 0.05a$	$0.0787 \pm 0.01b$	0.6481	$2.2 \pm 0.1b$	<0.001
R_A	C	0.1787	0.0974	0.5249	2.65a	<0.001
	N	0.3911	0.0931	0.4848	2.54a	<0.001
R_H	C	$0.2473 \pm 0.06a$	$0.0843 \pm 0.01a$	0.7924	$2.32 \pm 0.2a$	<0.001
	N	$0.1827 \pm 0.08a$	$0.0874 \pm 0.01a$	0.6003	$2.41 \pm 0.3a$	<0.001

Values are mean \pm SD (n = 4). Different letters mean significant difference between treatments at $P < 0.05$

highly associated with the supply of photosynthates (Högberg et al. 2001; Bahn et al. 2008). In this study, Q_{10} values of R_A and R_H were 2.65 and 2.32, respectively, in unfertilized treatment (Table 1). This is consistent with the result of shading-decreased Q_{10} of SR. Higher Q_{10} of R_A than that of R_H agrees with previous studies (Gaumont-Guay et al. 2008; Ni et al. 2012; Ma et al. 2013). Gaumont-Guay et al. (2008) suggested R_A was closely correlated with gross ecosystem photosynthesis, thus a photosynthetic enhancement of R_A resulted in the higher apparent Q_{10} value at the seasonal time scale.

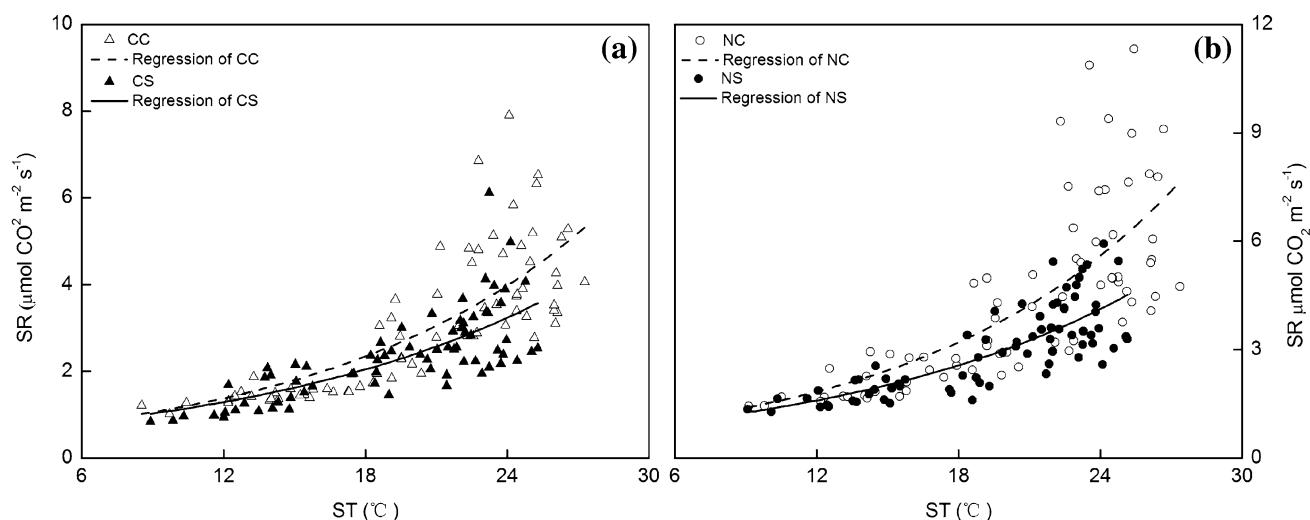
Addition of N reduced mean growing season R_H by 27 % ($P < 0.05$), while it increased R_A by 106 % ($P < 0.01$), resulting in a significant increase in SR by 42 % ($P < 0.01$) in un-shaded treatment (Fig. 1a). The stimulation of SR by N addition was attributed to greater increase in R_A and less inhibition of R_H , which agrees with several studies reported for grasslands (Yan et al. 2010;

Zhou et al. 2014), but our result counters the contention that N addition reduced SR and R_A in forest (Olsson et al. 2005; Sun et al. 2014). Higher contribution of R_A and younger tree age in this study than in other forest studies may explain the difference. Addition of N significantly increased maximum photosynthesis rates (A_{\max}) by 55 % ($P < 0.01$) and 52 % ($P < 0.01$) in un-shaded and shaded treatments, respectively (Table 2). Greater photosynthesis resulting from N addition led to significant increases in fine-root, coarse-root, leaf and stem biomass (Table 2). Therefore, the N-induced enhancement of R_A was due to increased photosynthesis, which might have supplied more carbon photosynthate for root and soil microbial activities (Carreiro et al. 2000; Xu and Wan 2008; Yan et al. 2010; Gao et al. 2014). The reduction in R_H after fertilization presumably resulted from the additional N retarding the decomposition of soil organic material by altering soil microbial communities (Allison et al. 2008) or limiting soil

Table 2 The mean maximum photosynthesis rate (A_{\max}) throughout the growing season, fine-root biomass, coarse-root biomass, leaf biomass and stem biomass in control (CC), shading (CS), N addition (NC) and shading plus N addition (NS) treatments

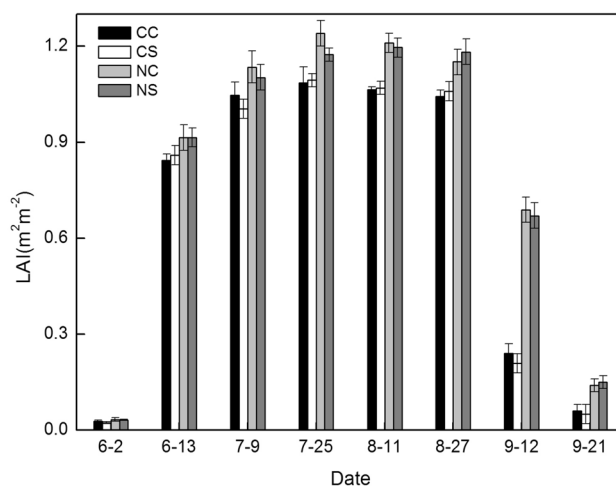
Treatments	A_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Fine-root biomass (g)	Coarse-root biomass (g)	Leaf biomass (g)	Stem biomass (g)
CC	$8.1 \pm 2.2\text{a}$	$49.6 \pm 4.5\text{a}$	$77.3 \pm 6.2\text{a}$	$20.0 \pm 3.1\text{a}$	$69.2 \pm 5.4\text{a}$
CS	$8.4 \pm 1.5\text{a}$	$53.26 \pm 5.2\text{a}$	$74.0 \pm 5.5\text{a}$	$18.9 \pm 2.7\text{a}$	$64.9 \pm 4.9\text{a}$
NC	$12.6 \pm 1.6\text{b}$	$75.8 \pm 4.3\text{b}$	$111.7 \pm 5.3\text{b}$	$28.0 \pm 3.3\text{b}$	$101.2 \pm 5.6\text{b}$
NS	$12.8 \pm 1.3\text{b}$	$70.6 \pm 6.1\text{b}$	$115.7 \pm 4.6\text{b}$	$25.5 \pm 3.4\text{b}$	$103.2 \pm 6.1\text{b}$

Different letters mean significant differences between treatments at $P < 0.05$ (mean \pm SD, $n = 4$)

**Fig. 2** Relationships between soil respiration and soil temperature in control (CC), shading (CS) treatments (a), and in N addition (NC) and shading plus N addition (NS) treatments (b). Values represent the mean of four replicates

microbial biomass and activity (Allen and Schlesinger 2004; Waldrop et al. 2004). N addition slightly reduced the Q_{10} of R_A (2.54) and increased the Q_{10} of R_H (2.41), while it had no significant effect on Q_{10} values of SR or its components (Table 1).

The shading effect on SR was strengthened by N addition, especially at low temperature. The declines in SR resulting from shading were 28, 38, 20 and 32 % in N addition treatment in the early, middle, late and total growing season, respectively (Fig. 1a). According to the regression lines between SR and soil temperature, the shading effect on SR was earlier and stronger in N-fertilized treatment than in unfertilized treatment at low temperature (Fig. 2). The leaf area indexes were larger ($P < 0.01$) in N addition treatments than in unfertilized treatments, especially in September (Fig. 3). Therefore, an N addition enhanced shading effect on SR caused by N addition possibly resulted from greater supply of

**Fig. 3** Overall mean (\pm SD) leaf area index (LAI) in control (CC), shading (CS), N addition (NC) and shading plus N addition (NS) treatments from 2 June to 21 September

photosynthates belowground in late growing season through higher photosynthesis, longer growing-season length and larger leaf area at low temperature (Table 1; Fig. 3).

Conclusion

Shading decreased SR, and the reduction had a seasonal characteristic. N addition stimulated SR and R_A but inhibited R_H . The positive response of SR to N addition mainly derived from significant increase in R_A by the stimulation of photosynthesis, which might have supplied more C substrate below ground. This conclusion is derived from the findings that photosynthesis, LAI and plant biomass were significantly enhanced by N addition. Furthermore, N addition strengthened the shading effect on soil respiration at low temperature because of greater photosynthate supply belowground in the late growing season through higher photosynthesis, longer growing-season length and larger leaf area. These results have important implications for linking soil respiration to photosynthesis when modelling long-term carbon exchange in forest ecosystems, especially in the context of N deposition.

Acknowledgments We thank the two anonymous reviewers for helpful comments on the manuscript. Funding was provided by the National Natural Science Foundation of China (41375119, 31400541) and the Key Laboratory of Forest and Soil Ecology (LFSE2013-11).

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