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Soil respiration and net ecosystem productivity in a chronosequence of hybrid poplar plantations

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Abstract: Forest stand age can affect ecosystem carbon (C) cycling and net ecosystem productivity (NEP). In Canada, establishment of short-rotation plantations on previously agricultural lands has been ongoing but the effect of stand development on soil respiration (R_s) and NEP in such plantations is poorly understood. This type of data is essential for constraining ecosystem models that simulate C dynamics over the rotation of a plantation. We studied R_s (including autotrophic, R_a , and heterotrophic, R_h) and NEP in 2008 and 2009 in a chronosequence of 5-, 8-, 14-, and 16-year-old (ages in 2009) hybrid poplar (*Populus deltoides* x *Populus x petrowskyana* var. Walker) plantations in northern Alberta. The highest R_s and NEP were generally found in the 14-year-old stand. Seasonal variations in R_s were similar among the plantations, with most of the variation explained by soil temperature at the 10 cm depth in 2008 with far less explained in 2009, a much drier year. In diurnal measurements, hysteresis was found between soil respiration and soil temperature, with the patterns of hysteresis different among stand ages. Soil respiration in the 14-year-old plantation had the greatest sensitivity to temperature changes. Stand age did not affect the R_h : R_s ratio, while the NEP exhibited strong inter-annual variability. We conclude that stand age was a major factor affecting R_s and NEP and such effects should be considered in empirical models used to simulate ecosystem C dynamics to evaluate potentials for C sequestration and the C source-sink relationship in short-rotation woody crop systems.

Key words: afforestation, carbon balance, chronosequence, stand age, temperature sensitivity

Introduction

Stand age can have a major effect on the net ecosystem productivity (NEP) of forests (Litvak et al., 2003; Grant et al., 2007a; Noormets et al., 2007; Black et al., 2009). The NEP is the balance between net primary productivity (NPP) and heterotrophic respiration (R_h) (Chapin et al., 2002), both of which change as stands develop. In the initial years after a forest plantation is established or a natural forest ecosystem is recovered from some form of disturbance, autotrophic respiration (or root respiration, R_a) and R_h , which is from the decomposition of plant residues and soil organic matter, are typically greater than carbon (C) dioxide (CO_2) uptake by photosynthesis (Amiro, 2001; Mkhabela et al., 2009), and thus the plantations would act as a net C source. With stand development, NPP increases rapidly due to quickly increased leaf area index and greater photosynthetic capacity of the trees, and R_h may decrease because of the depletion of easily decomposable substrates and lack of major new labile C supply (Grant et al., 2007a); the net result might be for the system to become a net C sink in late rotation plantations. As forest stands mature, NPP declines due to decreased soil nutrient availability, increased stomatal limitation, or a shift in the balance between photosynthesis and respiration in the production of plant tissues (Gower et al., 1996), the forests might become a smaller C sink, C neutral, or even a C source again (He et al., 2012).

Much research has been conducted on how NEP changes with stand age in natural (Thuille and Schulze, 2006; McMillan et al., 2008) or managed forests (Noormets et al., 2007; Black et al., 2009; Karu et al., 2009) after disturbances, e.g., logging, fire, or mining. For example, Litvak et al. (2003) found that after fire, the C sink capacity of boreal black spruce (*Picea mariana* (Mill.) B.S.P.) stands in central Manitoba increased in 11- to 36-year-old stands and then decreased to zero in 130-year-old stands, based on research on a chronosequence

consisting of 11-, 19-, 36-, 70- and 130-year-old stands. Zha et al. (2009) similarly found that after harvest, boreal jack pine (*Pinus banksiana* Lamb.) stands turned into C sinks from sources at age 29, and then the C sink capacity declined with age, based on a chronosequence with 2-, 10-, 29-, and 90-year-old stands. Using both biometric and eddy-covariance methods in a chronosequence (6-, 19-, 34- and 69-year-old) of white pine (*Pinus strobus* L.) forests, Peichl et al. (2010b) also observed that NEP was greater in the 19-year-old pine forest and decreased in the two older forests.

Soil respiration, which includes R_a and R_h , is a major contributor to the forest C balance (Ryan and Law, 2005; Gaumont-Guay et al., 2009). Forest development has a significant influence on soil respiration (Wiseman and Seiler, 2004; Saiz et al., 2006; Tedeschi et al., 2006; Ball et al., 2007), with the following patterns reported in the literature: 1) total soil respiration (R_s) increased with stand age to peak at an intermediate age and then decreased in a boreal black spruce chronosequence with 4-, 7-, 13-, 21-, 38-, 72- and 152-year-old stands (Bond-Lamberty et al., 2004b) and in a chronosequence of deciduous hardwood forests with 0-, 10-, 26-, 73- and 350-year-old stands that had different dominant species in each age category in Wisconsin and Michigan, respectively (Tang et al., 2009); 2) R_s decreased with stand age until 31 years old and then levelled off in older stands over a chronosequence with 10-, 15-, 31-, and 41-year-old first rotation Sitka spruce (*Picea sitchensis*) plantations in central Ireland (Saiz et al., 2006); 3) R_s decreased with stand age in 1-, 5-, 10- and 17-year-old coppiced oak (*Quercus cerris* L.) stands in central Italy (Tedeschi et al., 2006); and 4) R_s was similar across a chronosequence of 4-, 17-, 32- and 67-year-old white pine forests in southern Ontario, Canada (Peichl et al., 2010a). Therefore, the effect of stand age on R_s is very much site- or stand type-specific.

In Canada, ongoing afforestation on previously agricultural land, especially planting of short-rotation woody crops such as hybrid poplars, has been considered as an effective way to mitigate net CO₂ emissions (FAO, 2004; Yemshanov et al., 2012). In northern Alberta, approximately 1,200 hectares of hybrid poplar plantations were established each year for a number of years, with the goal of establishing a total of 10,000 ha on 20- to 25-year rotations, to supplement wood supply for pulp and paper mills (Hayward, Pers. Comm. 2014, Alberta-Pacific Forest Industries Inc.), while 6000 ha of hybrid poplar plantations had been established in other locations across Canada (Dominy et al., 2010). Establishment of hybrid poplar plantations at such a scale will have significant implications not only for wood supply in the region but also for the C balance and its feedback on the regional climate. However, little research on the effects of afforestation and the subsequent stand development on R_s and NEP has been carried out on these plantations established on previously agricultural lands (Saurette et al., 2006; 2008). In this region, Saurette et al. (2006) studied the stand age effect on R_s on four sites with different aged hybrid poplar (*Populus deltoides* x *Populus x petrowskyana* var. Walker) plantations using a static chamber system, reporting that R_s increased with stand age. Similarly, Arevalo et al. (2010) observed that R_s in a 9-year-old Walker hybrid poplar plantation was greater than that of a 2-year-old hybrid poplar plantation in northern Alberta, within the same ecological region to that of our study site and Saurette et al. (2006). The manual and infrequent measurements in Arevalo et al. (2010) (also limited to only two stand ages) and Saurette et al. (2006), however, could not sufficiently account for the R_s of the whole growing season. In addition, the temperature sensitivity of R_s could not be adequately tested when R_s measurements were limited to a few points in the growing season. The diurnal variations of R_s in the hybrid poplar plantations were also not thoroughly studied. Most importantly, Saurette et al. (2006; 2008) did not investigate

how NEP changes with stand age. A comprehensive study conducted in the same region using the eddy covariance method covered NEP but only for the first five years of a hybrid poplar plantation, which was enough time to show the shift from a net C source to a net C sink (Cai et al., 2011).

In the current study, we used automated chamber systems to measure R_s every two hours to investigate: 1) changes in R_s and its temperature sensitivity in different aged hybrid poplar plantations, 2) the patterns of seasonal and diurnal variations of R_s in the plantations, particularly on understanding how temperature controls the seasonal dynamics and diurnal changes of R_s , and 3) the inter-annual variability of NEP and changes in NEP with stand age to examine the age at which hybrid poplar stands shift from a net C source to a net C sink with the short-rotation plantations. Therefore, this work represents incremental research above Saurette et al. (2008) by providing more frequent soil respiration data and calculating the NEP (which was not done in Saurette et al., 2008), and above Cai et al. (2011) by extending the NEP calculations to 14-year-old stands, covering ~70% of the rotation of hybrid poplar plantations (based on a 20- to 25-year rotation).

Methods

Site description

The study site was located near the Alberta-Pacific Forest Industries Inc. (Al-Pac) pulp mill (54°49'N, 113°31'W), in the southern border of the Boreal Mixedwood ecological subregion in northern Alberta, Canada. The climate in this area is continental, with warm summers and long, cold winters. The growing season is about 175-180 days, from May to October (Government of Alberta, 2006). Climate normals between 1971 and 2000 showed that mean annual temperature

and precipitation in this area were 2.1 °C and 503.7 mm (including snow fall), respectively (Environment Canada, 2004). Of the two years this research was conducted, weather in this area was somewhat warmer and drier in 2009 than in 2008 during the growing season (air temperature 15.2 vs. 14.8 °C and precipitation 134.9 vs. 161.2 mm in 2009 vs. 2008) (Environment Canada, 2010). Trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* Voss), and jack pine on upland terrain were the dominant native tree species in this area (Natural Regions Committee, 2006). Level to gently undulating plain was the primary landform and the dominant soil type was Gray Luvisol (Soil Classification Working Group, 1998), with Dystric and Eutric Brunisols occurring in the coarse textured soil areas; those soils were the most common ones in the study area (Natural Regions Committee, 2006).

Four different aged hybrid poplar (Walker) plantations were selected for this study: Field 28S (F28S) planted in 2004 (5-year-old in 2009), Field 28N (F28N) planted in 2001 (8-year-old in 2009), Field 1 (F1) planted in 1993 (16-year-old in 2009), and Field 8 (F8) planted in 1995 (14-year-old in 2009). All plantations had trees planted at 3 x 3 m spacing (or about 1100 stems ha⁻¹) with trees in the 5-, 8-, 14- and 16-year-old stands about 5, 7, 14 and 16 meters tall, respectively, in 2009. Due to logistical (power supply) problems to operate the equipment in F1, this site was abandoned in 2009; the problem with the power supply was caused by the crown closure at the F1 site which resulted in reduced light penetration through the canopy and as a result, the solar panels did not generate enough power to operate the automated R_s measurement systems. The data generated in 2008 were reliable, as we did not have power supply issues. As such, not enough data were collected from this site in 2009 for a comprehensive analysis. All selected plantations were established on previously marginal agricultural land and had high

variability in soil organic C and nitrogen content (Saurette et al., 2006; Teklay and Chang, 2008). Soil C and nitrogen, and field capacity (or water holding capacity) in field F1 were much lower than those in the other fields, and its texture was also much coarser (Table 1). The soils at the four sites were classified as Gleysolic soils (Saurette et al., 2006) and other soil characteristics in these four different aged plantations can be found in Saurette et al. (2006) and Teklay and Chang (2008).

Root exclusion treatments to determine heterotrophic respiration rates

Two root-exclusion and two control (non-root exclusion) plots (1 x 1 m) were established in each plantation in late May 2009 to allow R_h rates to be quantified. The root exclusion and the control plots were located in the middle of a tree row, as this location represented the mean respiration rate in the 3 x 3 m planting pattern (Saurette et al., 2006). The root-exclusion plots were set up by trenching soil to a 50 cm depth to sever live tree roots, given that most root biomass and activity typically occur within the first 50 cm layer of the soil, based on a whole-tree root excavation study near these sites (Saurette et al., unpublished data). The trench was lined with a polypropylene landscaping fabric, which allowed water to move through but excluded roots from penetrating into the trenched plots. The trenches were backfilled with excavated soil. Control plots with no trenching were established adjacent to the root-exclusion plots within the same tree row. While the entire plantation other than the small root-exclusion plots can be viewed as the control plot, the 1 x 1 m non-trenched plot established beside each root exclusion plot makes the respiration measurements the most comparable between the two plots.

Soil respiration measurement

Soil respiration was measured using a non-steady state automated chamber system (ACS) custom made by the Biometeorology and Soil Physics Group in the Faculty of Land and Food Systems at the University of British Columbia (Jassal et al., 2005; Jassal et al., 2008). Soil respiration was measured from June to early November in 2008 and June to early October in 2009. During the 2008 measurement period, each ACS was equipped with three chambers (52.5 cm internal diameter, 50 L volume) with dome-shaped transparent lids; all three chambers were used for the control plots as the measurement in the root exclusion plots started in 2009. In 2009, each ACS was equipped with four chambers, two placed in the control plots and two in the root exclusion plots, within each stand age of the chronosequence. The transparent chamber lids were covered with a layer of dark paper followed by a layer of aluminum foil and the aboveground understory vegetation in the chambers was cut every two weeks. The collars were inserted about 5 cm into the soil and were anchored to the soil with long L-shaped metal bars. The chamber volume used for the calculation described below was corrected for chamber floor variations. The chambers were closed sequentially for one minute every two hours for measuring the rate of R_s using an infrared gas analyzer (IRGA, LI820 CO₂/H₂O analyzer). At each measurement cycle, the CO₂ concentration within the chamber was determined every second for one minute. The rate of change in CO₂ mole fraction in the chamber headspace starting 30 s after the closing of the chamber, which was found to be linear over time, was used to calculate the efflux (Jassal et al., 2005). The 30 s lead-time allowed the system to stabilize and the sample to reach the IRGA before taking measurements. The slope of the CO₂ concentration increase over time was derived using linear regression and the rate of R_s ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was calculated using the following equation:

$$R_s = \rho_a * (V/A) * (ds_c/dt)$$

where ρ_a is the dry air density in the chamber headspace (mol m^{-3}), V is the chamber volume (m^3), A is the area covered by the chamber (m^2), and ds_c/dt is the change rate of the CO_2 mixing ratio in the headspace over the measurement time. The air in the system was not scrubbed of water vapour, and the CO_2 mixing ratio (volume of CO_2 per volume of dry air) was not measured; instead, the volume of CO_2 per volume of air (including water vapour) was measured. This causes a small error when R_s was calculated using the equation above. The lids were kept open when the chambers were not in use to allow rain and litter to fall into the collar area.

Mean R_h throughout the growing season in 2008 was calculated using the R_h : R_s ratio of 0.63 determined by Saurette et al. (2008) for four different aged hybrid poplar plantations in the same area as our study. In 2009, in order to remove soil respiration caused by decomposition of severed fine roots in the trenched plots, a correction factor of 0.83 (Saurette et al., 2008) was used. Decomposition of fine roots in the trenched plots likely occurred immediately after they were severed, with the rate of loss of fine root mass initially fast and then slowing down in a two-phase decay pattern observed in many forests (McClaugherty et al., 1984). Mean R_h throughout the growing season in 2009 was calculated using mean R_s in the root exclusion plots multiplied by the correction factor.

As the daily winter air temperature can be -40°C or lower and usually hover around -15°C (Government of Alberta, 2006), it was not possible to measure R_s in the winter period (November to April), both R_a and R_h in the non-growing season was estimated using a process-based ecosystem model “ecosys” (Grant, 2001), which was calibrated for the study sites (Shi, 2010). The R_h is the key parameter needed to allow NEP to be calculated from NPP data. In the

“ecosys” model, R_h in each soil layer is controlled by the decomposition of soil organic matter, and calculated by the biomass of active heterotrophic microbial populations multiplied by a temperature dependent specific oxidation rate (Grant, 2001; Grant et al., 2006; Grant et al., 2007b). Air temperature during the non-growing season was used as input for the “ecosys” model to generate the hourly R_a and R_h (output) data; the air temperature data were retrieved from the nearest Alberta Environment weather station to the study site. Air temperature is correlated to soil temperature and was easier to obtain and was therefore used to calibrate the “ecosys” model. While the R_a and R_h from the “ecosys” modeling was used to supplement the field measured data, the analysis below will be focused on measured data.

Net primary productivity and NEP

A 15 x 15 m plot (with 25 trees) was established in each plantation for tree measurement. Diameter at breast height (DBH, cm) and total height (H, m) were measured for each tree in the plot at the beginning and end of the 2008 and 2009 growing seasons. The aboveground biomass (AGB, kg per tree) without leaves was determined using the biomass equation below (Table S1):

$$AGB = 0.6298 \times DBH^{1.3582} \times H^{0.2353}$$

The root biomass (RB, kg per tree, oven-dry weight) for the two younger plantations was calculated using the equation below (Table S1):

$$RB = 1.1810 \times DBH^{2.5123} \times H^{-2.1616}$$

The information on tree number, dry biomass, stem size and root size on the above two biometric equations is provided in Table S2.

Considering the RB equation developed in Table S1 was for younger plantations (Table S2), the RB for the two older plantations was calculated as follows (Fang et al., 2007). This RB equation was developed for poplar plantations in a temperate region but was the only biomass equation we could find for older polar trees. Biomass values calculated from biomass equations represent approximations of the real biomass.

$$RB = \exp(3.97 - 252.92 / (DBH * H))$$

Thirteen round litter traps with an internal diameter of 30 cm were randomly distributed in each plot to collect litterfall (LF, kg m⁻²) every month from August to November in each year. The collected LF was oven-dried at 65 °C until constant weight and weighed in the laboratory. The C content of the aboveground biomass, root and litterfall was calculated by multiplying a standard factor of 0.5 (Bond-Lamberty et al., 2004a; Pregitzer and Euskirchen, 2004; Arevalo et al., 2009). The NPP equals the difference in biomass C between the beginning and the end of the growing season plus litterfall:

$$NPP = (AGB + RB)_{\text{end of growing season}} - (AGB + RB)_{\text{beginning of growing season}} + LF$$

where AGB and RB were scaled-up from kg C tree⁻¹ to Mg C ha⁻¹ by multiplying by the number of trees planted per hectare, and LF was scaled-up from kg C per litter trap to Mg C ha⁻¹ by converting the litter trap area into a hectare; NPP, or the C flux over the growing season, is

expressed in $\text{Mg C ha}^{-1} \text{ yr}^{-1}$ considering that NPP would change little during the non-growing season.

The NEP ($\text{Mg C ha}^{-1} \text{ yr}^{-1}$) is then determined using the following equation:

$$\text{NEP} = \text{NPP} - R_h.$$

where R_h was scaled-up from $\mu\text{mol m}^{-2} \text{ s}^{-1}$ to $\text{Mg C ha}^{-1} \text{ yr}^{-1}$. The propagated error of NEP was calculated by adding together the standard error of NPP and R_h (Bond-Lamberty et al., 2004a).

Soil temperature, soil water content measurement and precipitation data

Soil temperature was measured every two hours at 5 cm and every hour at 10 cm depth with a 20 gauge extension copper-constantan thermocouple wire (Omega Engineering, Montreal, QC) placed adjacent to the chambers. The data were logged with Campbell Scientific CR10X dataloggers (Logan, UT). Volumetric water content at 10 and 20 cm depths was measured every hour using Campbell Scientific CS616 water content reflectometers (Logan, UT) and datalogged with a CR10X datalogger. Precipitation data were retrieved from the nearest (~100 km) Alberta Environment weather station (Rich Lake, 54.5°N, 116.6°W) to the study site.

Data analysis

The relationship between daily mean R_s and T_s at 10 cm soil depth was analyzed by the following Q_{10} model (Qi et al., 2002):

$$R_s = R_{s10} * Q_{s10}^{(T_s-10)/10}$$

where R_s is the soil respiration rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), R_{s10} is the soil respiration rate at 10 °C, Q_{s10} is the temperature sensitivity of R_s , which is defined as the relative increase in R_s for a 10 °C increase in soil temperature, and T_s is soil temperature (°C) measured at 10 cm soil depth. We evaluated whether the model fit (R^2) can be improved by using T_s at 5 vs. at 10 cm depth in this equation. However, R^2 was not improved. Therefore, the relationship between R_s and T_s at 5 cm soil depth was not presented.

For data analysis, the normality of distribution and homogeneity of variance of the data sets were tested using SAS 9.0 (Version 9.0, SAS institute Inc.). The difference in R_s among the different aged plantations over the measurement period was tested using repeated measures ANOVA (one-way) at a significance level of $\alpha = 0.05$ in SAS 9.0. Linear and multiple regression analyses were also conducted using SAS 9.0. The multiple regression model of soil respiration against T_s and soil water content in the 0-10 cm layer was conducted in the form of $R_s = a \times W_s^2 + b \times W_s + c \times d^{((T_s-10)/10)} + e$, which provides the best fit for the data, where W_s and T_s are soil water content and soil temperature, respectively, and a, b, c, d and e are coefficients from fitting the regression model to the data. Linear and nonlinear curve fitting were done in Origin (Version 8.0, OriginLab Corp.).

Results

Soil temperature and soil water content

Soil temperature at 10 cm depth followed similar seasonal trends in the different aged hybrid poplar plantations throughout the growing season in the two years (Fig. 1). However, seasonal trends of T_s were different among the two years with different peak times in each of the growing

seasons (Fig. 1a and 1b). Soil temperature was consistently lower in older plantations until T_s peaked and became warmer in the older stands than in the younger stands thereafter.

Soil water content at 10 cm depth was higher in the two younger (5- and 8-year-old) than in the older plantations (14- and 16-year-old) during the growing seasons, with similar seasonal trends among the plantations (Fig. 1c and 1d). There was a substantial drawdown of soil water content by transpiration of the trees in the two older stands (Fig. 1).

Seasonal variation of soil respiration

Similar seasonal variations of R_s among the different aged plantations were observed in each year (Fig. 2). However, the patterns of seasonal variation in 2008 (Fig. 2a) were different from that in 2009 (Fig. 2b), with different peak times in the growing seasons. In 2008, R_s in the 14-year-old plantation was significantly higher than that in the other three plantations in June and July ($p < 0.05$) (no data available in June in the 16-year-old plantation), but not in August, September or October (Fig. 2a). No difference in R_s was found among the 5-, 8- and 16-year-old plantations in 2008 (Fig. 2a). In 2009, R_s in the 14-year-old plantation was higher than that in the 5- and 8-year-old plantations ($p < 0.05$), except that in June no difference was observed between the 5- and 14-year-old plantations; the R_s was also different between the 5- and 8-year-old plantations in June ($p = 0.01$), but not in the other months (Fig. 2b).

Most of the non-growing season R_s in all plantations calculated using the “ecosys” model was below $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ in both years (Fig. 2). Several peaks of R_s were shown in early spring prior to leaf-out. During the non-growing season R_s accounted for $19 \pm 1\%$ (mean $\pm$ SE) of the annual R_s (Fig. 2).

An exponential relationship between daily mean R_s and T_s at 10 cm was found in all the studied plantations (Fig. 3). The T_s at 10 cm explained less of the variation of R_s in 2009 than in 2008 (Fig. 3). In 2009, more of the variation in R_s was accounted for by T_s in the older plantations (14- and 16-year-old) than in the younger ones (5- and 8-year-old). The Q_{s10} values were the highest in the 14-year-old plantations in both 2008 and 2009 among the plantations.

A positive linear relationship ($P < 0.05$) between R_s and soil water content were found in the 5-year-old plantation in 2008 (Fig. 4a). A quadratic polynomial relationship ($P < 0.05$) between R_s and soil water content was also found in the 14-year-old plantation in 2008 and 2009 (Fig. 4b and 4c). A multiple regression analysis was performed and showed that the R^2 was much greater when soil water content was incorporated for 2009 (Table 2), a year when T_s stayed fairly constant and might not have been a limiting factor for R_s .

Heterotrophic soil respiration in growing season of 2009

Soil respiration in the trenched plots, referred to as R_h , had similar seasonal trends to R_s in all three plantations in the growing season (Fig. 5). Respiration rates between June and October were different between the control and root exclusion treatments in each of the three plantations ($P < 0.01$). The R_h was greater in the 14- than in the 5- and 8-year-old plantations. No difference in R_h was found between the 5- and 8-year-old plantations (Fig. 5). The R_h accounted for 66, 70, and 66%, after the correction factor of 0.83 was applied (assuming that the effect of plantation age on the proportion of fine root decomposed is minimal), of R_s in the 5-, 8- and 14-year-old plantations, respectively, and seasonal patterns of the R_h : R_s ratios varied among these three plantations over the measurement period (Fig. S1).

Soil temperature at the 10 cm depth had an exponential relationship with R_s in both the control and root exclusion treatments (Fig. 6). The R_{s10} and Q_{s10} values in the control treatment were always greater than those in the root exclusion treatment in all the plantations, indicating that the R_a had a greater temperature sensitivity than R_h .

Diurnal variation of soil respiration

In 2008, bihourly measured R_s increased from early morning (around 8 h) and reached a maximum in late afternoon (around 15 - 17 h) in the two younger plantations (Fig. 7a and b) or late evening (around 22 h) in the two older plantations (Fig. 7c and d). The peak of bihourly R_s was 3 h earlier than that of T_s in the 5-year-old plantation, and the identical pattern of bihourly R_s is the same as T_s in the 8- and 16-year-old plantation. In the 14-year-old plantation, the maximum bihourly R_s lagged behind T_s by 2 h. In 2009, bihourly R_s in the control and root exclusion treatments both increased from early morning (around 8 h) and peaked in early afternoon (around 12-14 h) in all three plantations (Fig. 7e, f and g). In contrast, root R_s (or R_a) increased from 18 h, peaked in the middle of the night (around 2 h) and levelled off in the daytime in the youngest plantation (Fig. 7e). No evident diurnal variation of root R_s was observed in the two older plantations (Fig. 7f and g). By plotting diurnal R_s and T_s , we found that different hysteresis behaviour occurred with stand age, with both clockwise and counter-clockwise hysteresis (Fig. S2).

Net ecosystem productivity

The NPP increased with plantation age with the 14-year-old plantation having the greatest amount of litterfall in both years (Fig. 8). The 14-year-old plantation had the largest R_h among

the studied plantations in both years. Net ecosystem productivity increased with plantation age in both years, with negative values in the two younger plantations in 2008 and all three studied plantations in 2009, and positive values in the older plantations in 2008.

Discussion

Soil respiration in the different aged plantations

Chronosequence studies are unfortunately almost always non-replicated at the stand age level. This study was conducted in a very small area with a flat terrain and soil conditions were relatively similar, but the reader is cautioned about the spatial variability of soils that existed and when interpreting the stand age effect, which we believed to be the dominant effect causing what we observed, we need to keep in mind the confounding effect of soil/site conditions on all parameters we evaluated. In general, R_s in the 16-year-old plantation was lower than that in the 14-year-old plantation in 2008, even though fine RB (reflecting the greatest standing biomass in that stand) and dissolved organic C content in the oldest stand was usually greater than that in the 14-year-old stand (Saurette et al., 2008; Teklay and Chang, 2008). The lower soil organic matter and soil water content and coarser soil texture could mute the effect of fine RB and dissolved organic C on R_s and result in lower R_s in the 16-year-old stand, when all other conditions were the same, for example, no obvious disease or herbivory issues were observed across the plantations.

In general, the increasing R_s with stand age in both years was consistent with that reported by Saurette et al. (2006) in similar stands, and with studies on hybrid poplars at another site in central Alberta (Arevalo et al., 2010), in a boreal black spruce chronosequence in Manitoba (Bond-Lamberty et al., 2004b), and in a loblolly pine (*Pinus taeda*) chronosequence

ranging from 1 to 25 years old (Wiseman and John, 2004). Our results show that stand age should be considered if empirical models are to be used to predict R_s in afforested sites.

The difference in R_s with stand age could be caused by many factors, such as differences in RB (Table 1), soil organic C and dissolved organic C content, and the amount of litterfall as a potential source of labile organic C input. Root biomass tends to increase with stand age particularly in the early part of the rotation and can cause the stand age effect on R_s (Wiseman and Seiler, 2004). Saurette et al. (2008) reported that fine RB increased with stand age (ranged from 4 to 13 years old) in hybrid poplar plantations. The contents of soil organic matter and dissolved organic C, both as potential substrates for microbial respiration, have been shown to increase with stand age in hybrid poplar plantations (Saurette et al., 2006; Teklay and Chang, 2008). In addition, a greater amount of litterfall input both above- and belowground in the older plantations would increase R_s through input of labile organic C (Yan et al., 2006).

Seasonal variation and temperature sensitivity of soil respiration

Seasonal variation in R_s was observed in the different aged plantations in both years in this study as would be expected (Rayment and Jarvis, 2000; Gaumont-Guay et al., 2006; Tang et al., 2009). In general, seasonal variation of R_s was driven by T_s , possibly modified by soil water content (Fig. 3 and 4), as further discussed below. In 2008, T_s explained most of the seasonal variation in R_s , while soil water content, which has been found to significantly influence R_s in some research (Davidson et al., 1998; Jassal et al., 2008), was not a limiting factor (mostly above $0.2 \text{ m}^3 \text{ m}^{-3}$) in our study in 2008. However, T_s only explained a small part of the variation in R_s in 2009, because T_s was less limiting in 2009 than in 2008 due to the relatively high and fairly stable temperature (daily mean temperature varied between 13 and 18 °C from June to late September

in 2009) over the growing season. Incorporating soil moisture content in a multiple regression improved the percent variation of R_s explained in 2009, depending on the age of the plantation (Table 2).

The R_s was greater in the 5-year-old than in the other plantations in 2009 (Fig. 2b). The result could be derived from temporal variation in spatial heterogeneity of abiotic (e.g., T_s , water and soil organic matter contents, and shading by tree canopy), biotic (e.g., activities of roots and organism) variables or their interactions. The non-growing season R_s accounted for 19% of annual R_s (Fig. 2), which is similar to what has been reported by McDowell et al. (2000) and Kurganova et al. (2003), with results in both of those studies based on modeling work. Kurganova et al. (2003) found that 21% of annual R_s was winter soil respiration in natural ecosystems of Russia's southern taiga soils and McDowell et al. (2000) observed that 17% of annual R_s occurred in winter time. The multiple R_s peaks that occurred in early spring in the non-growing season were associated with spring thaw of soil (Elberling et al., 2008), during which many restrictions of R_s , such as soil water content and T_s (as compared with the deep winter) are alleviated, and there was a flush of dissolved organic C supplied as a microbial energy source in the soil.

Temperature sensitivity of R_s as measured by Q_{s10} was different among the stand ages, generally increasing with stand age, which is consistent with Ma et al. (2014) in *Larix principis-rupprechtii* plantations (ranging from 10 to 40 years old) in northern China and Tedeschi et al. (2006) in Mediterranean oak forests (ranging from 1 to 17 years old) in central Italy. The greater Q_{s10} in the 14-year-old stand in both years suggested that different dominant components (root and heterotrophic respiration) were probably involved in different plantations. The Q_{s10} values in the current study were well within the range of 2.0 - 6.3 for Q_{s10} reported by Davidson et al.

(1998) and Janssens et al. (2003) for European and North-American forest ecosystems. Our Q_{s10} values are similar to what was reported for a boreal aspen stand (3.8) in Canada (Gaumont-Guay et al., 2006) and an aspen-birch (*Populus davidiana* Dode and *Betula platyphylla* Suk.) forest (3.75) in northeastern China (Wang et al., 2006). The largest Q_{s10} value in the 14-year-old plantation (the expected rotation length of such hybrid poplar plantations is around 20-25 years) suggests that the older stands studied in this paper had a greater sensitivity to temperature changes and might be more sensitive to future climate warming scenarios in terms of CO₂ emissions. However, when a plantation is in a substrate-limited condition, warming did not increase R_s in either field (Luo et al., 2001) or lab incubation experiments (Teklay et al., 2010). The Q_{10} value has been found to vary with both time and space (Xu and Qi, 2001; Janssens et al., 2003). When R_s is simulated using the Q_{10} model, selection of Q_{10} value would be dependent on the objective of the modeling. If the model output is short-term respiration, the short-term Q_{10} should be used, avoiding over- or under-estimation (Xu and Qi, 2001; Jia et al., 2014). If a model is used to predict R_s in a large landscape area, spatially varied Q_{10} values are required for accurate simulation modeling. Therefore, considering the variation in temperature sensitivity of R_s with stand age, empirical models should consider stand age effect when temperature sensitivity is used to predict soil CO₂ efflux.

Diurnal variations of soil respiration

Hysteresis in the R_s - T_s relationship is one of the issues still unresolved in understanding the temperature response of R_s in different ecosystems (Jia et al., 2014). Hysteresis was found between R_s and T_s at 10 cm depth in the diurnal measurements in the 14-year-old plantations in both years, similar to what Gaumont-Guay et al. (2006) and Tang et al. (2005) reported.

Gaumont-Guay et al. (2006) found that the peak of R_s was 3-5 hours later than that of T_s at 2 cm depth. Tang et al. (2005) also observed that hourly R_s decoupled with T_s at 8 cm depth. They all suggested that diurnal variation of rhizospheric respiration caused the hysteresis. Rhizospheric respiration responds to the transport of photosynthates from leaves to roots, and time is needed for photosynthate transportation. In addition, abrupt decreases in R_s rates were observed in the early morning in different aged plantations. One potential reason was that the C sink competition among different tree components was switched (Gaumont-Guay et al., 2008). For example, when C supply is scarce, shoots are a strong sink for the C supply than roots (Minchin and Lacomte, 2005), as is the case when plants prepare to resume photosynthesis in the morning. In contrast, some other studies found that diurnal variation of R_s was in-phase with T_s (Drewitt et al., 2002; Shi et al., 2006) as is the case with what we found in the intermediate-aged plantation (8-year-old).

The most interesting part of hysteresis in this study for both years was that in the younger plantation (5-year-old) the peak of R_s occurred earlier than that of T_s , in the intermediate plantation (8-year-old); in the oldest plantation (16-year-old) R_s changes in pace with T_s ; and in the 14-year-old plantations R_s lagged a few hours after changes in T_s . There are several possible explanations for these results. First, in the young plantations, the effect of delay of transporting photosynthates might not be as significant as in older plantations because of the shorter tree height or distance for conducting the photosynthates from the crown to the roots (Kuzyakov and Gavrichkova, 2010); second, the clockwise hysteresis in the 5-year-old plantation might suggest that CO_2 production is from the deeper soil (Gaumont-Guay et al., 2006). In the 14-year-old plantation, the counter-clockwise hysteresis might be caused by the time used for transporting photosynthates, heat transport damped by soils, and the time used to transport CO_2 produced

from deep soil to the soil surface individually or together (Phillips et al., 2011). However, the counter-clockwise hysteresis was not observed in the oldest plantation (16-year-old); the low soil water content and coarse soil texture in the 16-year-old stand might attenuate the effect of heat transport damp and CO₂ transportation (Phillips et al., 2011).

The diurnal variation of soil respiration reported in this study is illustrative of the different patterns in hysteresis among plantations of different ages; the measurements were not conducted on the same dates but in roughly the same period in the two years and the number of replications were generally low due to limitation to having access to only 12 automated chambers; however, that should not diminish the usefulness of this dataset as the weather on the same day in different years is likely to be different regardless. Jia et al. (2014) observed lags between R_s and T_s at 10 cm depth at both the seasonal and the diel scales in a *Pinus tabulaeformis* plantation in northern China; at the diel scale, hysteresis was found in the early and late growing seasons, but not in the summer. The seasonality in the lags between R_s and T_s was due to the use of a single T_s measurement depth that fails to represent seasonal changes in the depth of CO₂ production. Further research is needed to fully understand the controls on the lag between R_s and T_s to reduce uncertainties in C cycle analysis.

Soil respiration in the trenched plot

The lack of stand age effect on the R_h : R_s ratio in this study was consistent with what Saurette et al. (2008) reported (average R_h : $R_s = 0.63$) involving four hybrid poplar plantations with different ages in the same study area. However, Bond-Lamberty et al. (2004b) and Tedeschi et al. (2006) found that stand age affected the R_a : R_s ratio (and thus the R_h : R_s ratio) in both a boreal black spruce and in a chronosequence of Mediterranean oak forests, but the effect was limited. The R_h :

R_s ratio in this study was much higher than those reported for boreal forests (Russell and Voroney, 1998; Bond-Lamberty et al., 2004b), even though it was less than the value (0.78) reported by Tedeschi et al. (2006) for Mediterranean oak forests. Soil organic matter content and tree growth would be major determinants of the R_h : R_s ratio, and we cannot expect similar values across sites or regions; however, the large R_h : R_s ratio could be an artefact. First, the decomposition of severed roots within the trenched plots may have had a greater contribution to R_h than what has been accounted for by the use of the correction factor (Gaumont-Guay et al., 2008). Second, the roots of the understory vegetation that regrow in the plots could also have contributed to the higher than expected R_h (Bond-Lamberty et al., 2004b), even though the aboveground understory vegetation was removed regularly. Third, reduced nitrogen uptake in the trenched plots could also affect R_h as greater nitrogen availability such as through nitrogen addition can suppress microbial respiration (Ramirez et al., 2010). In addition, the trenched plots may have more soil water available for microbial activities due to reduced transpiration rates. Therefore, the values reported in this study may reflect the upper limit of R_h : R_s ratio for the studied systems.

The R_h : R_s ratio was greater than 60% throughout the growing season in this study in all plantations. This was in contrast with Gaumont-Guay et al. (2008) who found that root respiration dominated R_s from mid-July to mid-September in a boreal black spruce stand they studied. The greatest R_s in the trenched plots in the 14-year-old plantation could be attributed to the greater soil organic C content, the greater amount of litterfall (Fig. S2) and a large pool of dissolved organic C that can be easily decomposed (Teklay and Chang, 2008).

Net ecosystem productivity in different aged plantations

Net ecosystem productivity increased with stand age in this study, with the two younger plantations acting as a net C source and the two older plantations as a net C sink. This result was similar to that of Litvak et al. (2003) and Zha et al. (2009). Litvak et al. (2003) found a C source-sink shift with stand age in five different aged black spruce stands (ranging from 11 to 130 years old). Zha et al. (2009) observed that jack pine stands turned into a C sink from a C source as stands aged and proposed that the change was due to the increased leaf area index along the chronosequence. The changes in NPP and NEP along the chronosequence in this study were consistent in both years, suggesting that the stand age effect on NEP was determined by NPP. The increasing NEP with stand age indicates that the older plantations have a greater capacity to sequester C.

However, NEP in this study was much smaller in 2009 than in 2008 for each studied plantation, attributable to the drier weather in 2009; summer drought is common in this area and water availability can substantially reduce stand productivity (Grant et al., 2006), which resulted in a lower NPP and a larger R_h . The strong inter-annual variability in the ecosystem C balance indicates that in future climate warming/drought scenarios, NEP could dramatically decrease. In order to better understand the warming/drought effects on NEP, future research should focus on simulating warming/drought scenarios in the field to test their effects on ecosystem C balance.

The reader is cautioned to the potential shortcomings in calculating NEP in this study. The equations used to calculate belowground biomass for the two older plantations were not localized and thus could have introduced errors, considering the site-specific nature of such biomass equations. Another issue was the way heterotrophic respiration was determined that might have caused an overestimation of R_h as discussed above. In addition, understory biomass was not assessed in this study which might contribute to NEP, especially in the younger

plantations that had an open canopy, even though the understory vegetation was vigorously controlled in the younger plantations as part of the plantation management regime. For example, the AGB of the understory vegetation was $1.47 \text{ Mg C ha}^{-1}$ in the 8-year-old plantation. Therefore, if the understory biomass was considered in calculating the NEP, the C source-sink relationship would need to be adjusted for each plantation age; in addition, we also need to recognize that the understory contributes to the root respiration dynamics, which varies among systems. The reader is also cautioned about the uncertainty associated with the estimates of the winter respiration rates from the “ecosys” model; since it was not possible to measure winter respiration rates with the equipment we had, estimating them using the calibrated “ecosys” model was the best option available. This is the first rotation of a hybrid poplar plantation established on former agricultural land and we would expect some legacy effect of agricultural soil organic C, especially in the early years after plantation establishment. Hence, successive poplar rotations will probably have different C and respiration dynamics. Further research to investigate C dynamic in successive rotations of poplar plantations is needed.

Conclusions

Seasonal variations of R_s in the studied hybrid poplar plantations were similar among the stand ages in a given year, with large inter-annual variations observed for each stand age. Soil temperature explained most of the intra-seasonal variation in 2008, a year with non-limiting soil water content. Our work indicates that air/soil temperature was the major control on R_s rates and that relationship was not affected by stand development within the range of stand ages we studied. The strong temperature control on R_s also means that the seasonal dynamics of R_s was not affected by stand age. Different time lag patterns were observed between diurnal variations of R_s and T_s in the different aged plantations and in different years. This has implications for

scaling up point R_s measurements made during the day (such as those using a static chamber system) to seasonal or annual R_s rates. Our study showed that both heterotrophic R_s and NPP generally increased with stand age but the latter increased at a faster rate, resulting in increased NEP with stand age. We conclude that the ecosystem C balance had strong inter-annual variability; it takes four to seven years for the hybrid poplar plantations to become a C sink, and the longer the rotation, the greater the potential for C sequestration by the plantations since the NEP increased with stand age. Future research should focus on calibrating or developing site-specific belowground biomass equations for older plantations to improve the accuracy of NPP calculations, to improve the methods for determining heterotrophic respiration rates, and to conduct on-site measurement of winter R_s rates to improve NEP estimates.

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Table 1. Soil bulk density, total carbon (C) content, total nitrogen (N) content, field capacity, root biomass and soil texture in the 0-10 cm soil in the different aged hybrid poplar plantations.

Plantation age	Bulk density (g cm ⁻³)	Total C (Mg m ⁻²)	Total N (Mg m ⁻²)	Field capacity (m ³ m ⁻³)	Root biomass (Mg C ha ⁻¹)	Soil texture
5-year-old	1.09	32.74± 4.72a	2.92±0.35a	0.45	0.44	Silt loam
8-year-old	1.09	28.14± 3.41a	2.56±0.36a	0.45	1.07	Silt loam
14-year-old	1.00	52.82± 7.65b	4.19±0.64b	0.40	9.96	Loam
16-year-old	1.29	19.25± 2.84c	1.78±0.27c	0.24	13.45	Sandy loam

Note: the different lowercase letters with C and N values indicate significant differences between different sites.

Table 2. Coefficients for the multiple regression model of soil respiration against soil temperature and soil water content at 10 cm depth in the form $R_s = a*W_s^2 + b*W_s + c*d^{((T_s-10)/10)} + e$ for the four hybrid poplar stands in 2008 and 2009 and R^2 from fitting soil respiration with soil temperature only. The units for R_s , W_s and T_s are $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $\text{m}^3 \text{ m}^{-3}$, and $^\circ\text{C}$, respectively.

Plantation age (year)	a	b	c	d	e	MSE	R^2 (model with W_s and T_s)	R^2 (model with T_s only)
2008								
5	41.98	28.34	1.91	1.82	5.61	0.12	0.80	0.79
8	-111.60	79.59	2.75	2.07	-15.72	0.13	0.84	0.82
14	-154.79	91.13	11.46	1.24	-22.14	0.56	0.75	0.68
16	-86.97	39.09	1.29	3.31	-4.49	0.08	0.88	0.87
2009								
5	—*	—	—	—	—	—	—	0.16
8	-56.10	38.63	0.48	6.32	-5.60	0.10	0.65	0.58
16	1.00	-1.00	0.10	0.19	-0.12	0.23	0.81	0.44

*: curve fitting using the equation $R_s = a*W_s^2 + b*W_s + c*d^{((T_s-10)/10)} + e$ cannot be accomplished.

MSE stands for mean square error.

Figure captions

Figure 1. Seasonal dynamics of daily mean soil temperature at 10 cm depth from June to

November in (a) 2008 and (b) 2009 and soil water content at 10 cm depth and precipitation from June to November in (c) 2008 and (d) 2009 in the different aged hybrid poplar plantations.

Figure 2. Seasonal dynamics of daily mean soil respiration (R_s) (a) from June to November in 2008 and (b) from June to early October in 2009. The small inserts in (a) and (b) are non-growing season R_s from November to May modelled using the “ecosys” model.

Figure 3. Relationships between daily mean soil respiration (R_s) and daily mean soil temperature (T_s) at 10 cm depth in different aged plantations in (a) 2008 and (b) 2009.

Figure 4. Relationships between daily mean soil respiration (R_s) and daily mean soil water content at 10 cm in different aged plantations: a) 5-year-old plantation in 2008, b) 14-year-old plantation in 2008, and c) 14-year-old plantation in 2009.

Figure 5. Seasonal variation of soil respiration in both control and root exclusion treatments from June to early October in 2009 in a) the 5-year-old plantation, b) the 8-year-old plantation, and c) the 14-year-old plantation. Vertical bars are SEs.

Figure 6. Relationship between daily mean soil respiration (R_s) in control and root exclusion treatments and daily mean soil temperature (T_s) at 10 cm in different aged plantations in 2009.

Figure 7. Diurnal variation of bihourly mean soil respiration (R_s) and bihourly mean soil temperature (T_s) at 10 cm in different aged plantations in 2008 (July 14 to August 12, a, b, c, d), and 2009 (June 16 to 28, e, f, g).

Figure 8 Annual net primary productivity (NPP), heterotrophic respiration (R_h), litterfall (LF) and net ecosystem productivity (NEP) in different aged plantations in 2008 and 2009. Vertical bars are SEs.

For Review Only

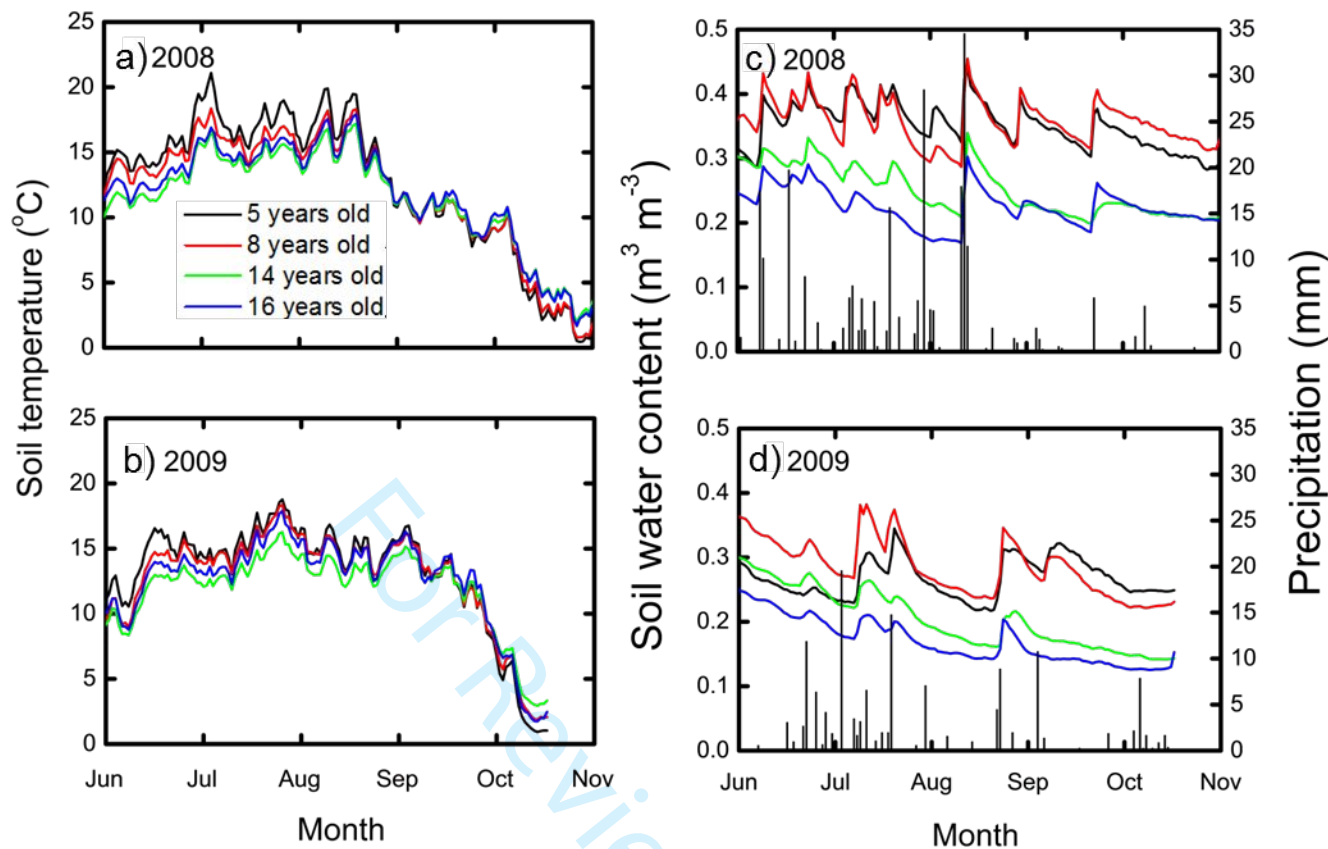


Fig. 1

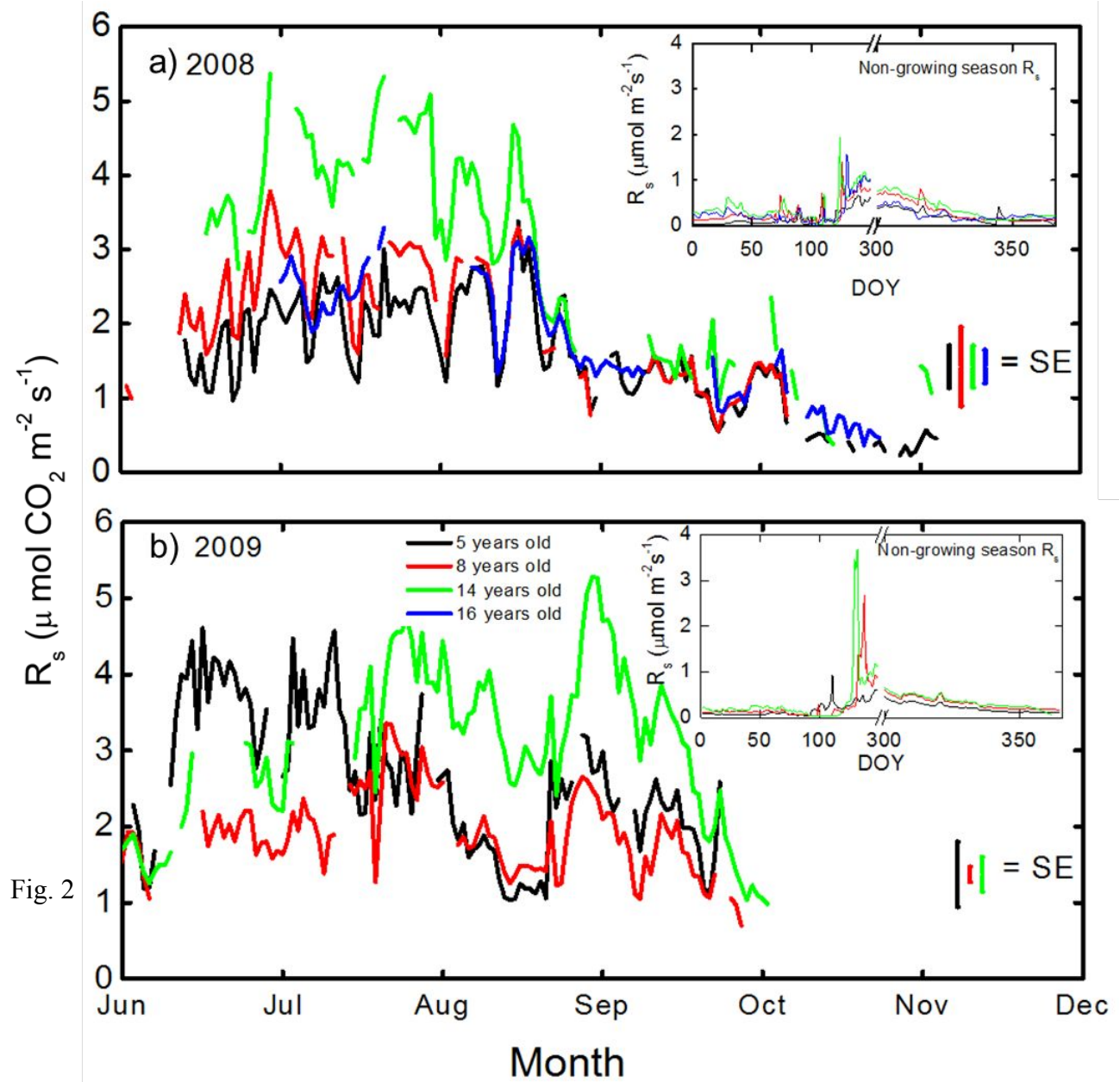


Fig. 2

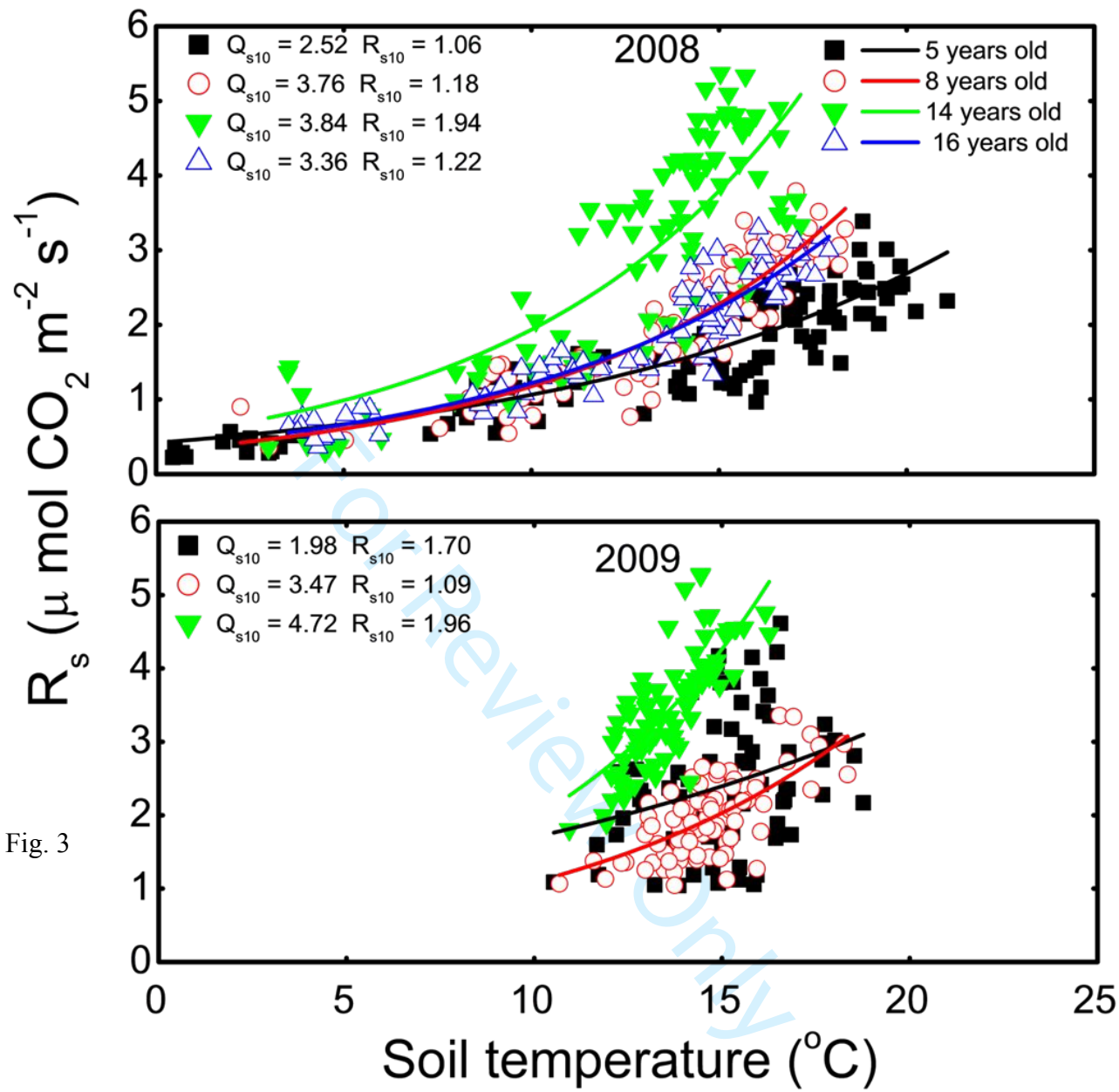


Fig. 3

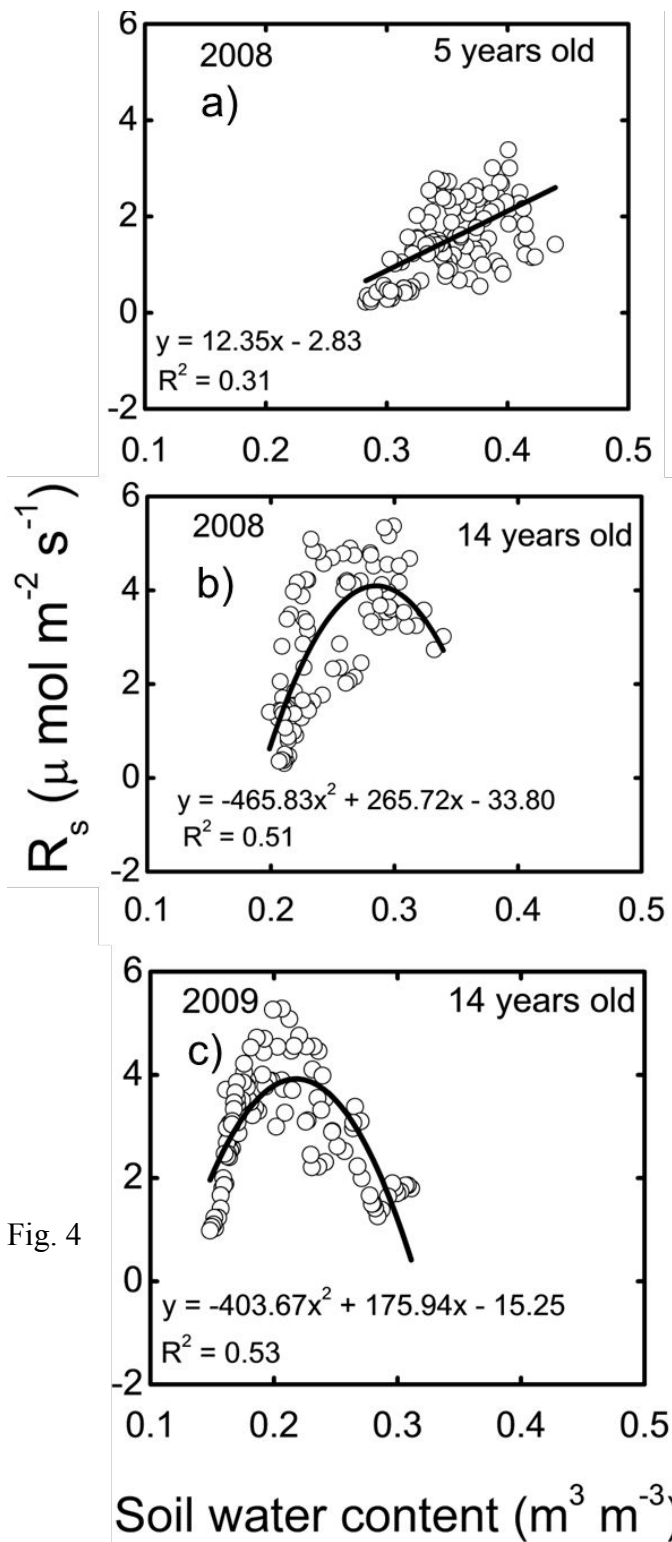


Fig. 4

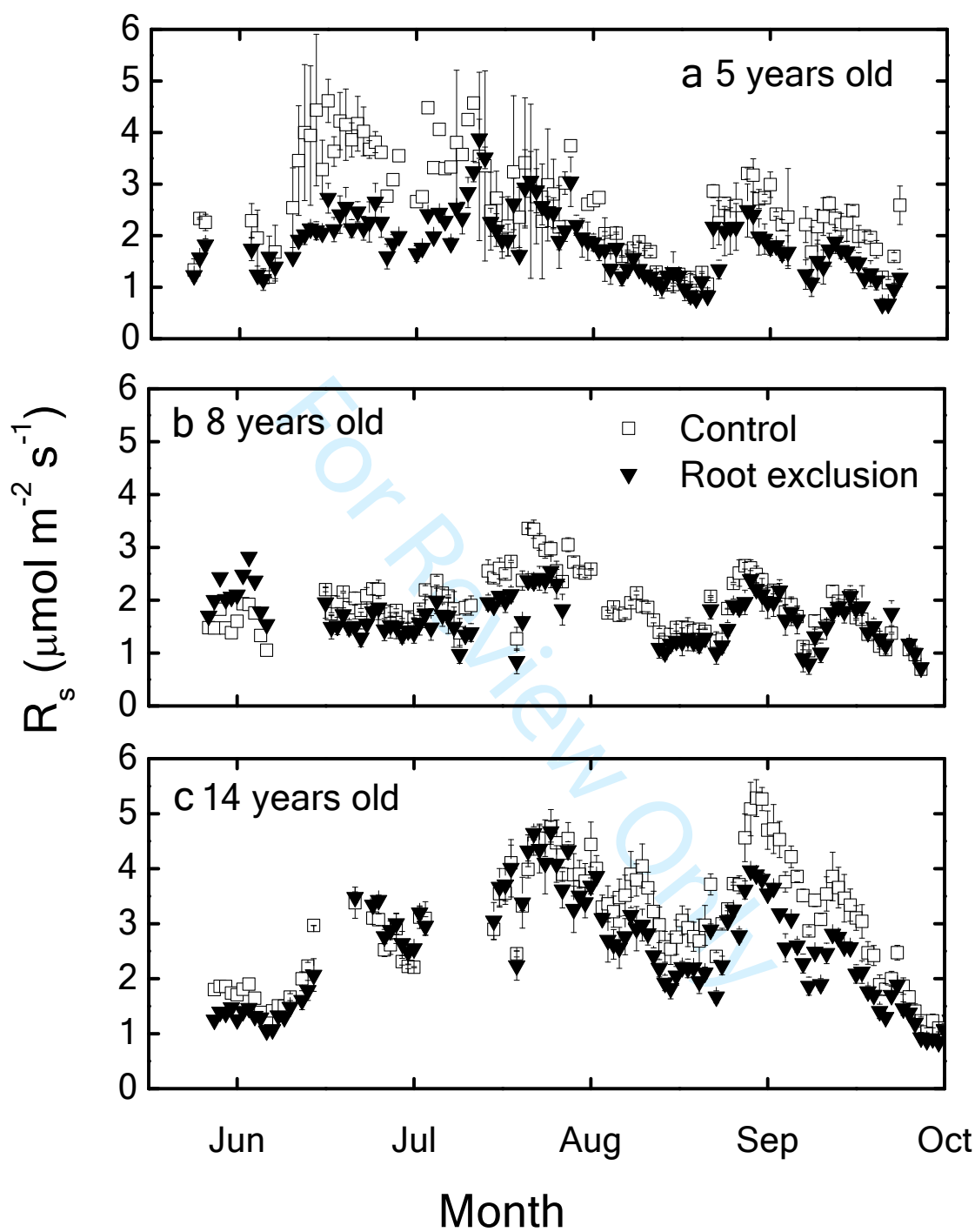


Fig. 5

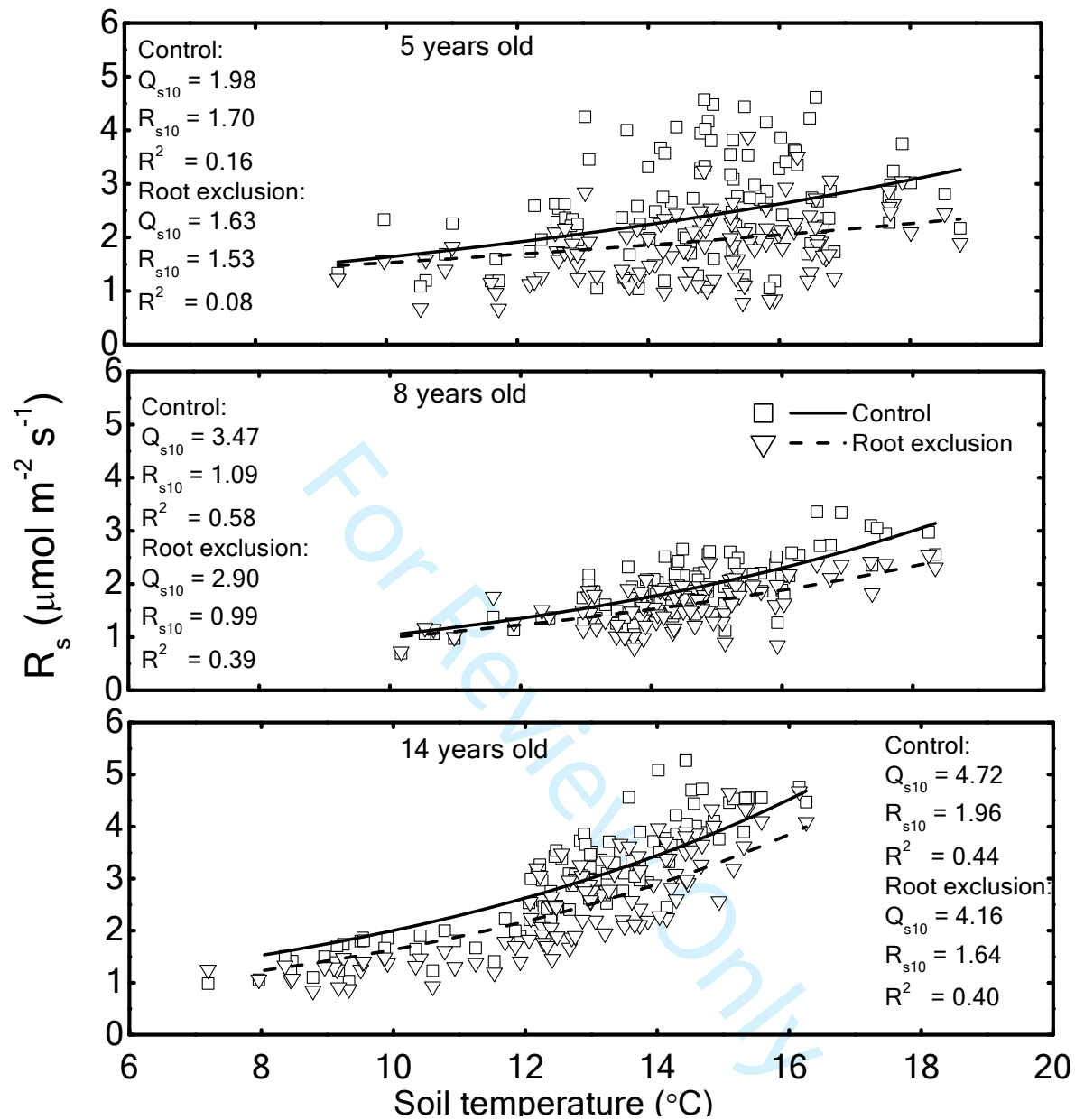


Fig. 6

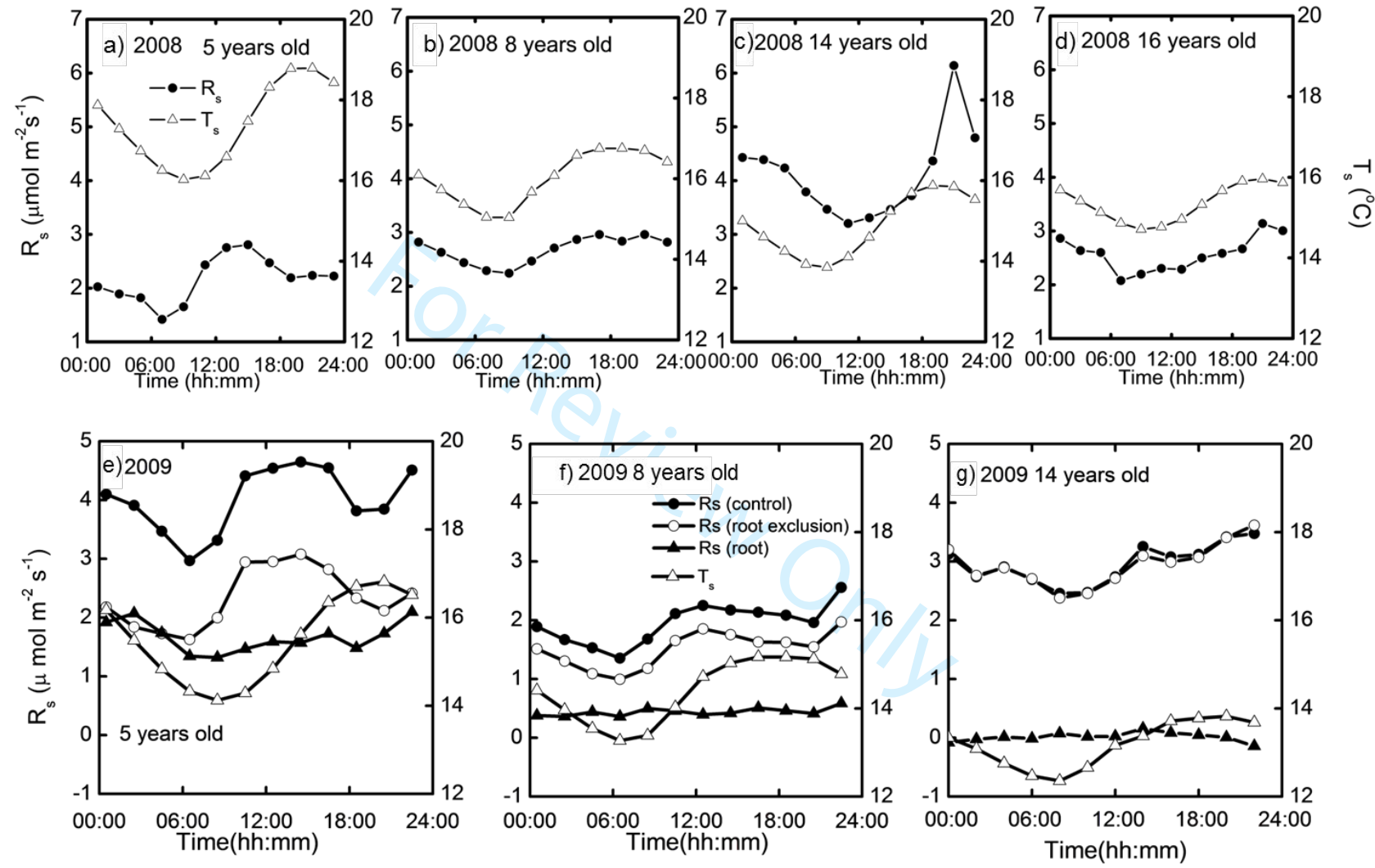


Fig. 7

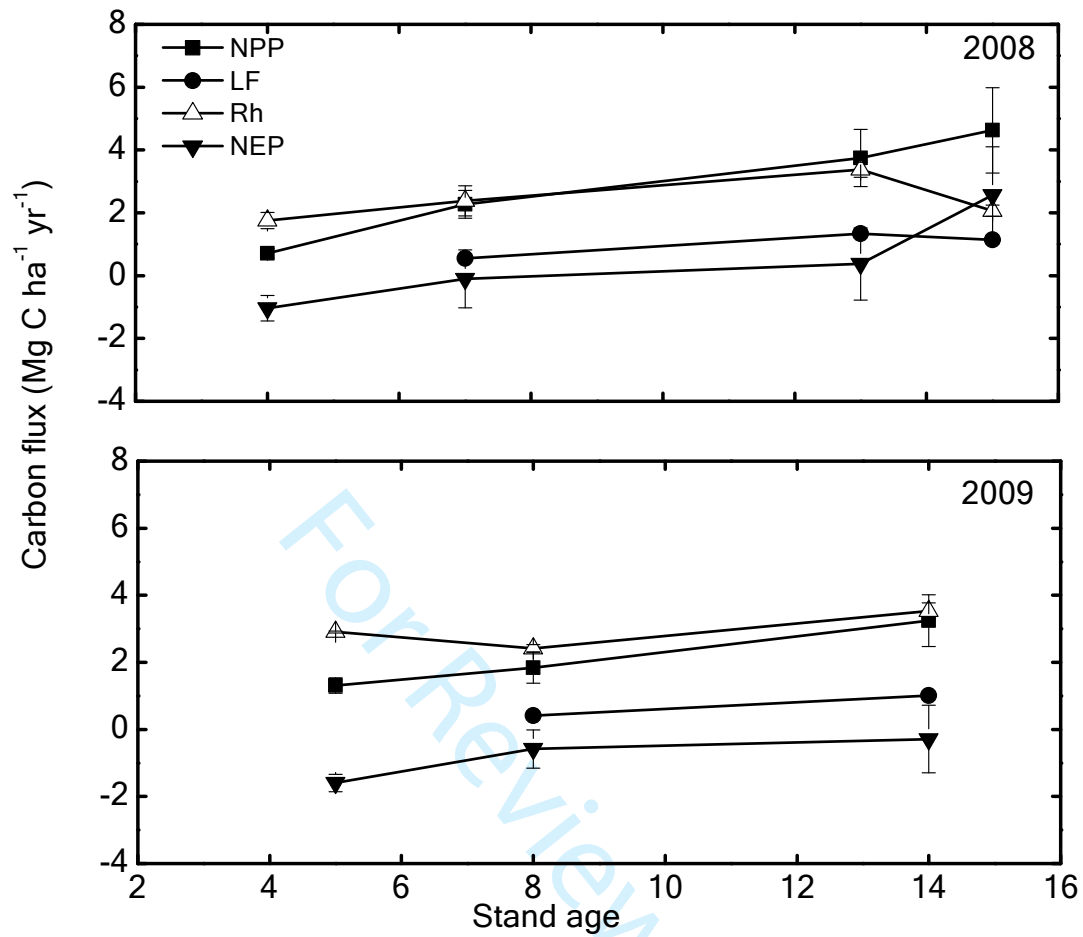


Fig. 8