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. These types of data are 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-yr-old (ages in 2009) hybrid poplar ($Populus deltoides \times Populus \times petrowskyana$ var. Walker) plantations in northern Alberta. The highest $R_s$ and NEP were generally found in the 14-yr-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-yr-old plantation had the greatest sensitivity to temperature changes. Stand age did not affect the $R_a/R_h$ ratio, whereas 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.

Résumé : L’âge d’un peuplement forestier peut affecter le cycle du carbone (C) et la productivité nette (PN) de l’écosystème. Au Canada, on pratique couramment l’assolement de plantations de courte durée sur des terres antérieurement cultivées sans qu’on se soit suffisamment attardé aux effets de tels peuplements sur la respiration du sol ($R_s$) et la PN. Or, ces données sont indispensables à la création de modèles de l’écosystème qui simuleraient la dynamique du C d’une plantation à l’autre. En 2008 et 2009, les auteurs ont étudié chronologiquement $R_s$ (y compris la respiration autotrophe, $R_a$, et la respiration hétérotrophe, $R_h$) et la PN de peuplements de peupliers hybrides ($Populus deltoides \times Populus \times petrowskyana$ var. Walker) de 5, 8, 14 et 16 ans (âge en 2009), dans le nord de l’Alberta. En général, les valeurs les plus élevées de $R_s$ et de PN ont été observées chez le peuplement de 14 ans. Les fluctuations saisonnières de $R_s$ sont similaires dans les différents peuplements. En 2008, ces variations s’expliquaient en grande partie par la température du sol à 10 cm de profondeur, mais il a été plus difficile d’y trouver une explication l’année suivante, qui était beaucoup plus aride. Quand on examine les relevés diurnes, on constate qu’il y a hystérèse entre la respiration et la température du sol. Cependant, l’hystérèse diffère avec l’âge du peuplement. Ainsi, le peuplement de 14 ans affiche la plus grande sensibilité aux variations de températures. L’âge du peuplement n’affecte pas le ratio $R_a/R_h$, mais la PN varie considérablement d’une année à l’autre. Les auteurs en concluent que l’âge du peuplement est un facteur important qui agit sur $R_s$ et la PN, et qu’on devrait en tenir compte dans les modèles empiriques qui simulent la dynamique du C dans l’écosystème dont on se sert pour évaluer les possibilités de séquestration du C et les liens entre les sources et les puits de C dans les assolements brefs de cultures ligneuses. [Traduit par la Rédaction]

Mots-clés : afforestation, bilan du carbone, séquence chronologique, âge du peuplement, sensibilité à la température.
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 $R_a$ 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-yr-old stands and then decreased to zero in 130-yr-old stands, based on research on a chronosequence consisting of 11-, 19-, 36-, 70-, and 130-yr-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-yr-old stands. Using both biometric and eddy-covariance methods in a chronosequence (6-, 19-, 34-, and 69-yr-old) of white pine (Pinus strobus L.) forests, Peichl et al. (2010b) also observed that NEP was greater in the 19-yr-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-yr-old stands (Bond-Lamberty et al. 2004b) and in a chronosequence of deciduous hardwood forests with 0-, 10-, 26-, 73-, and 350-yr-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 yr old and then levelled off in older stands over a chronosequence with 10-, 15-, 31-, and 41-yr-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-yr-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-yr-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 $CO_2$ emissions (FAO 2004; Yemshanov et al. 2012). In northern Alberta, approximately 1200 ha 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 20–25 yr rotations, to supplement wood supply for pulp and paper mills (A. Hayward, personal communication, Alberta-Pacific Forest Industries Inc., St. Albert, AB, Canada), whereas 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 $R_a$ 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 $R_a$ on four sites with different-aged hybrid poplar (Populus deltoides × Populus × petrowskyana var. Walker) plantations using a static chamber system, reporting that $R_a$ increased with stand age. Similarly, Arevalo et al. (2010) observed that $R_a$ in a 9-yr-old Walker hybrid poplar plantation was greater than that of a 2-yr-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 $R_a$ of the whole growing season. In addition, the temperature sensitivity of $R_a$ could not be adequately tested when $R_a$ 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 5 yr 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 2 h 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 (Cai et al. 2011) by extending the NEP calculations to 14-yr-old stands, covering ~70% of the rotation of hybrid poplar plantations (based on a 20–25 yr rotation).

Materials and 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 d, 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 snowfall), respectively (Environment Canada 2004). Of the 2 yr 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-yr-old in 2009), Field 28N (F28N) planted in 2001 (8-yr-old in 2009), Field 1 (F1) planted in 1993 (16-yr-old in 2009), and Field 8 (F8) planted in 1995 (14-yr-old in 2009). All plantations had trees planted at 3 m × 3 m spacing (or about 1100 stems ha⁻¹) with trees in the 5-, 8-, 14-, and 16-yr-old stands about 5, 7, 14, and 16 m 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 (N) content (Saurette et al. 2006; Teklay and Chang 2008). Soil C and N 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 m × 1 m) were established in each plantation in late May 2009 to allow $R_s$ 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 m × 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 (D.D. 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. Although the entire plantation other than the small root-exclusion plots can be viewed as the control plot, the 1 m × 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, 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 2 wk. 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 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 1 min every 2 h for measuring the rate of cumulative 30 s lead-time allowed the system to stabilize, and the rate of CO2 concentration increase over time was derived using linear regression, and the sample to reach the IRGA before taking measurements. The slope of the CO2 concentration change in the 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:

\[
R_s = \rho_a \times (V/A) \times (\text{d}s/\text{dt})
\]

where \( \rho_a \) is the dry air density in the chamber headspace (\( \text{mol m}^{-2} \)), \( V \) is the chamber volume (\( \text{m}^3 \)), \( A \) is the area covered by the chamber (\( \text{m}^2 \)), and \( \text{d}s/\text{dt} \) is the change rate of the CO2 mixing ratio in the headspace over the measurement time. The air in the system was not scrubbed of water vapour, and the CO2 mixing ratio (volume of CO2 per volume of dry air) was not measured; instead, the volume of CO2 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, 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 \( R_h \) in the winter period (November to April), both \( R_s \) 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, 2007b). Air temperature during the non-growing season was used as input for the “ecosys” model to generate the hourly \( R_s \) 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. Although the \( R_s \) and \( R_h \) from the “ecosys” modeling were used to supplement the field

### 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-yr-old       | 1.09                          | 32.74 ± 4.72a            | 2.92 ± 0.35a              | 0.45                                | 0.44                          | Silt loam    |
| 8-yr-old       | 1.09                          | 28.14 ± 3.41a            | 2.56 ± 0.36a              | 0.45                                | 1.07                          | Silt loam    |
| 14-yr-old      | 1.00                          | 52.82 ± 7.65b            | 4.19 ± 0.64b              | 0.40                                | 9.96                          | Loam         |
| 16-yr-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.
measured data, the analysis below will be focused on measured data.

Net primary productivity and NEP

A 15 m × 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 above-
ground biomass (AGB, kg·tree⁻¹) without leaves was
determined using the biomass equation below (Supplementary Table S1²):

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

The root biomass (RB, kg·tree⁻¹, oven-dry weight) for
the two older plantations was calculated using the
equation below (Supplementary Table S1²):

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

The information on tree number, dry biomass, stem
size, and root size on the above two biometric equations
is provided in Supplementary Table S2².

Considering the RB equation developed in
Supplementary Table S1² was for the two older plantations (Supplementary Table S2²), the RB for the two
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 approxima-
tions of the real biomass.

\[
RB = \exp(3.97 - 252.92/(DBH \times H))
\]

A total of 13 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
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 stan-
dard 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 converting the litter trap area into a
hectare; NPP, or the C flux over the growing season, is
expressed in Mg C·ha⁻¹·yr⁻¹ considering that NPP would
change little during the non-growing season.

The NEP (Mg C·ha⁻¹·yr⁻¹) is then determined using the
following equation:

\[
\text{NEP} = \text{NPP} - R_h
\]

where \( R_h \) was scaled-up from \( \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) to
Mg C·ha⁻¹·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 2 h at 5 cm and
every hour at 10 cm depth with a 20 gauge extension
copper–constantan thermocouple wire (Omega
Engineering, Montreal, QC, Canada) placed adjacent to
the chambers. The data were logged with Campbell
Scientific CR10X dataloggers (Logan, UT, USA).
Volumetric water content at 10 and 20 cm depths was
measured every hour using Campbell Scientific CS616
water content reflectometers (Logan, UT, USA) 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):

\[
R_s = R_{s10} \times Q_{10}^{(T_s - 10)/10}
\]

where \( R_s \) is the soil respiration rate (\( \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( R_{s10} \)
is the soil respiration rate at 10 °C, \( Q_{10} \) 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 evalu-
ated 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 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 analysis of variance (one-way) at a significance
level of \( \alpha = 0.05 \) in SAS version 9.0. Linear and multiple
regression analyses were also conducted using SAS

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²Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjss-2020-0006.
version 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 2 yr (Fig. 1). However, seasonal trends of $T_s$ were different among the 2 yr with different peak times in each of the growing seasons (Figs. 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-yr-old) than in the older plantations (14- and 16-yr-old) during the growing seasons, with similar seasonal trends among the plantations (Figs. 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-yr-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-yr-old plantation) but not in August, September, or October (Fig. 2a). No difference in $R_s$ was found among the 5-, 8-,
and 16-yr-old plantations in 2008 (Fig. 2a). In 2009, \( R_s \) in the 14-yr-old plantation was higher than that in the 5- and 8-yr-old plantations \( (P < 0.05) \), except that in June, no difference was observed between the 5- and 14-yr-old plantations; the \( R_s \) was also different between the 5- and 8-yr-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 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) 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% ± 1% (mean ± standard error) 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-yr-old) than in the younger ones (5- and 8-yr-old). The \( Q_{10} \) values were the highest in the 14-yr-old plantations in both 2008 and 2009 among the plantations.

A positive linear relationship \( (P < 0.05) \) between \( R_s \) and soil water content was found in the 5-yr-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-yr-old plantation in 2008 and 2009 (Figs. 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-yr-old plantations. No difference in \( R_h \) was found between the 5- and 8-yr-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-yr-old plantations, respectively, and seasonal patterns of the \( K_h \): \( R_s \) ratios varied among these three plantations over the measurement period (Supplementary 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 \( R_{10} \) and \( Q_{10} \) values in the control treatment were always greater than those...
in the root exclusion treatment in all the plantations, indicating that the $R_s$ 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 (Figs. 7a and 7b) or late evening (around 22 h) in the two older plantations (Figs. 7c and 7d). The peak of bihourly $R_s$ was 3 h earlier than that of $T_s$ in the 5-yr-old plantation, and the identical pattern of bihourly $R_s$ is the same as $T_s$ in the 8- and 16-yr-old plantation. In the 14-yr-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.

### 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 $R_s = a \times W_s^2 + b \times W_s + c \times d^{(T_s-10)/10} + e$ for the four hybrid poplar stands in 2008 and 2009 and $R^2$ from fitting soil respiration with soil temperature only.

| Plantation age (year) | $A$   | $b$   | $c$   | $d$   | $e$   | MSE | $R^2$ |
|----------------------|-------|-------|-------|-------|-------|-----|-------|
| 2008                 |       |       |       |       |       |     |       |
| 5                    | 41.98 | 28.34 | 1.91  | 1.82  | 5.61  | 0.12| 0.80  |
| 8                    | −111.60 | 79.59 | 2.75  | 2.07  | −15.72 | 0.13| 0.84  |
| 14                   | −154.79 | 91.13 | 11.46 | 1.24  | −22.14 | 0.56| 0.68  |
| 16                   | −86.97 | 39.09 | 1.29  | 3.31  | −4.49  | 0.08| 0.88  |
| 2009                 |       |       |       |       |       |     |       |
| 5                    | —     | —     | —     | —     | —     | —   | —     |
| 8                    | −56.10 | 38.63 | 0.48  | 6.32  | −5.60  | 0.10| 0.65  |
| 16                   | 1.00  | −1.00 | 0.10  | 0.19  | −0.12  | 0.23| 0.81  |

Note: The units for $R_s$, $W_s$, and $T_s$ are $\mu$mol CO$_2$·m$^{-2}$·s$^{-1}$, m$^3$·m$^{-3}$, and °C, respectively. Curve fitting using the equation $R_s = a \times W_s^2 + b \times W_s + c \times d^{(T_s-10)/10} + e$ cannot be accomplished. MSE, mean square error.
In contrast, root Rs (or Ra) 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 Rs was observed in the two older plantations (Figs. 7f and 7g). By plotting diurnal Rs and Ts, we found that different hysteresis behaviour occurred with stand age, with both clockwise and counter-clockwise hysteresis (Supplementary Fig. S2).

**Net ecosystem productivity**

The NPP increased with plantation age with the 14-yr-old plantation having the greatest amount of litterfall in both years (Fig. 8). The 14-yr-old plantation had the largest Rn 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, Rn in the 16-yr-old plantation was lower than that in the 14-yr-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-yr-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 Rs, and result in lower Rs in the 16-yr-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 Rs 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 yr old (Wiseman and Seiler 2004). Our results show that stand age should be considered if empirical models are to be used to predict Rs in afforested sites.

The difference in Rs 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 Rs (Wiseman and Seiler 2004). Saurette et al. (2008) reported that fine RB increased with stand age (ranged from 4 to 13 yr 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 Rs through input of labile organic C (Yan et al. 2006).

Seasonal variation and temperature sensitivity of soil respiration

Seasonal variation in Rs was observed in the different-aged plantations in both years in this study as would be expected (Raymo and Jarvis 2000; Gaumont-Guay et al. 2006; Tang et al. 2009). In general, seasonal variation of Rs was driven by T, possibly modified by soil water content (Figs. 3 and 4), as further discussed below. In 2008, T explained most of the seasonal variation in Rs, whereas soil water content, which has been found to significantly influence Rs in some research (Davidson et al. 1998; Jassal et al. 2008), was not a limiting factor (mostly above 0.2 m m−3) in our study in 2008. However, T only explained a small part of the variation in Rs in 2009 because T 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 Rs explained in 2009, depending on the age of the plantation (Table 2).

The Rs was greater in the 5-yr-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, 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 Rs accounted for 19% of annual Rs (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 Rs was winter soil respiration in natural ecosystems of Russia’s southern taiga soils and McDowell et al. (2000) observed that 17% of annual Rs occurred in winter time. The multiple Rs 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 Rs, such as soil water content and T (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 Rs as measured by Q 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 yr old) in northern China and Tedeschi et al. (2006) in Mediterranean oak forests (ranging from 1 to 17 yr old) in central Italy. The greater Qs in the 14-yr-old stand in both years suggested that different dominant components (root and heterotrophic respiration) were probably involved in different plantations. The Q values in the current study were well within the range of 2.0–6.3 for Q reported by Davidson et al. (1998) and Janssens et al. (2003) for European and North-American forest ecosystems. Our Q 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 value in the 14-yr-old plantation (the expected rotation length of such hybrid poplar plantations is around 20–25 yr) 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 Rs in either field (Luo et al. 2001) or laboratory incubation experiments (Teklay et al. 2010). The Q value has been found to vary with both time and space (Xu and Qi 2001; Janssens et al. 2003). When Rs is simulated using the Q model, selection of Q value would be dependent on the objective of the modeling. If the model output is short-term respiration, the short-term Qs should be
used, avoiding over- or under estimation (Xu and Qi 2001; Jia et al. 2013). 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 CO\(_2\) 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. 2013). Hysteresis was found between \( R_s \) and \( T_s \) at 10 cm depth in the diurnal measurements in the 14-yr-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 h 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 photosynthe transport. 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 Lacointe 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-yr-old).

The most interesting part of hysteresis in this study for both years was that in the younger plantation (5-yr-old) the peak of \( R_s \) occurred earlier than that of \( T_s \), in the intermediate plantation (8-yr-old); in the oldest plantation (16-yr-old) \( R_s \) changes in pace with \( T_s \); and in the 14-yr-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 Gavrishkova 2010); second, the clockwise hysteresis in the 5-yr-old plantation might suggest that CO\(_2\) production is from the deeper soil (Gaumont-Guay et al. 2006). In the 14-yr-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-yr-old); the low soil water content and coarse soil texture in the 16-yr-old stand might attenuate the effect of heat transport damp and CO\(_2\) 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 2 yr 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. (2013) 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 CO\(_2\) 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 \( R_{th}/R_s \) ratio in this study was consistent with what Saurette et al. (2008) reported (average \( R_{th}/R_s = 0.63 \)) 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 \( R_{th}/R_s \) ratio (and thus the \( R_{th}/R_s \) ratio) in both a boreal black spruce and in a chronosequence of Mediterranean oak forests, but the effect was limited. The \( R_{th}/R_s \) 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 \( R_{th}/R_s \) ratio, and we cannot expect similar values across sites or regions; however, the large \( R_{th}/R_s \) ratio could be an artefact. First, the decomposition of severed roots within the trenched plots may have had a greater contribution to \( R_{th} \) 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 \( R_{th} \) (Bond-Lamberty et al. 2004b), even though the aboveground understory vegetation was removed regularly. Third, reduced N uptake in the trenched plots could also affect \( R_{th} \) as greater N availability such as through N 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 $R_h$ in the trenched plots in the 14-yr-old plantation could be attributed to the greater soil organic C content, the greater amount of litterfall (Supplementary 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 yr 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. 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 Mg C ha$^{-1}$ in the 8-yr-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; because 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 $R_h$ 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 $R_h$ rates, and that relationship was not affected by stand development within the range of stand ages we studied. The strong temperature control on $R_h$ also means that the seasonal dynamics of $R_h$ was not affected by stand age. Different time lag patterns were observed between diurnal variations of $R_h$ and $T_h$ in the different-aged plantations and in different years. This has implications for scaling up point $R_h$ measurements made during the day (such as those using a static chamber system) to seasonal or annual $R_h$ rates. Our study showed that both heterotrophic $R_h$ 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 4–7 yr 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 because 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 $R_h$ rates to improve NEP estimates.
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References

Amiro, B.D. 2001. Paired-tower measurements of carbon and energy fluxes following disturbance in the boreal forest. Glob. Change Biol. 7: 253–268. doi:10.1046/j.1365-2486.2001.00398.x.

Arevalo, C.B.M., Bhatti, J.S., Chang, S.X., and Sidders, D. 2009. Ecosystem carbon stocks and distribution under different land-uses in north central Alberta, Canada. For. Ecol. Manage. 257: 1776–1785. doi:10.1016/j.foreco.2009.01.034.

Arevalo, C.B.M., Bhatti, J.S., Chang, S.X., Jassal, R.S., and Sidders, D. 2010. Soil respiration in four different land use systems in north central Alberta, Canada. J. Geophys. Res. 115: G01003. doi:10.1029/2009G010006.

Ball, T., Smith, K.A., and Moncريف, J.B. 2007. Effect of stand age on greenhouse gas fluxes from a Sitka spruce [Picea sitchensis (Bong.) Carr.] chronosequence on a peaty gley soil. Glob. Change Biol. 13: 2128–2142. doi:10.1111/j.1365-2486.2007.01427.x.

Black, K., Byrne, K.A., Mencuccini, M., Tobin, B., Nieuwenhuis, M., Reidy, B., et al. 2009. Carbon stock and stock changes across a Sitka spruce chronosequence on surface-water gley soils. Forestry, 82: 255–272. doi:10.1093/forestry/cpp005.

Bond-Lamberty, B., Wang, C.K., and Gower, S.T. 2004a. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Glob. Change Biol. 10: 473–487. doi:10.1111/j.1365-2486.2003.0742.x.

Bond-Lamberty, B., Wang, C.K., and Gower, S.T. 2004b. Contribution of root respiration to soil surface CO2 flux in a boreal black spruce chronosequence. Tree Physiol. 24: 1387–1395. doi:10.1093/treephys/24.12.1387.

Cai, T.B., Price, D.T., Orchansky, A.L., and Thomas, B.R. 2011. Carbon, water, and energy exchanges of a hybrid poplar plantation during the first five years following planting. Ecosystems, 14: 658–671. doi:10.1007/s10021-011-9436-8.

Chapin, F.S., Pamela, A.M., and Mooney, H.A. 2002. Principles of terrestrial ecosystem ecology. Springer-Verlag New York, Inc. pp. 140–145.

Davidson, E.A., Belk, E., and Boone, R.D. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Glob. Change Biol. 4: 217–227. doi:10.1046/j.1365-2486.1998.00128.x.

Dominy, S.W.J., Gilsenan, R., McKenney, D.W., Allen, D.J., Hatton, T., Koven, A., et al. 2010. A retrospective and lessons learned from Natural Resources Canada’s Forest 2020...
He, I.M., Chen, J.M., Pan, Y.D., Birdsey, R., and Kattge, J. 2012. Relationships between net primary productivity and forest stand age in U.S. forests. Glob. Biogeochem. Cycle, 26: GB3009. doi:10.1029/2010GB003942.

Janssens, I., Dore, S., Epron, D., Lankreijer, H., Buchmann, N., Longdoz, B., et al. 2003. Climatic influences in seasonal and spatial differences in soil CO2 efflux. Pages 235–255 in R. Valentini, ed. Fluxes of carbon, water and energy of European forests. Vol. 163. Ecological Studies. Springer, Berlin, Germany.

Jassal, R., Black, A., Novak, M., Morgenstern, K., Nesic, Z., and Gaumont-Guay, D. 2005. Relationship between soil CO2 concentrations and forest-floor CO2 effluxes. Agric. For. Meteorol. 130: 176–192. doi:10.1016/j.agromet.2005.03.005.

Jassal, R.S., Black, T.A., Novak, M.D., Gaumont-Guay, D., and Nesic, Z. 2008. Effect of soil water stress on soil respiration and its temperature sensitivity in an 18-year-old temperate Douglas-fir stand. Glob. Change Biol. 14: 1305–1318. doi:10.1111/j.1365-2486.2008.01573.x.

Jia, X., Zha, T., Wu, B., Zhang, Y., Chen, W., Wang, X.P., et al. 2013. Temperature response of soil respiration in a Chinese pine plantation: hysteresis and seasonal vs. diel Q10. PLoS ONE, 8(2): e57858. doi:10.1371/journal.pone.0057858. PMID:23469089.

Karhu, H., Szava-Kovats, R., Pensa, M., and Kull, O. 2003. Annual and seasonal CO2 fluxes from Russian southern taiga soils. Tellus Ser. B 55(2): 220–228. doi:10.1016/S0304-3800(01)00506-3.

Kuzyakov, Y., and Gavrichkova, O. 2010. REVIEW: Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls. Glob. Change Biol. 16: 3386–3406. doi:10.1111/j.1365-2486.2010.01279.x.

Littvak, M., Miller, S., Wofsy, S.C., and Goulden, M. 2003. Effect of stand age on whole ecosystem CO2 exchange in the Canadian boreal forest. J. Geophys. Res. Atmos. 108(D3). doi:10.1029/2002JD002854.

Luo, Y.Q., Wan, S.Q., Hui, D.F., and Wallace, L.L. 2001. Acclimatization of soil respiration to warming in a tall grass prairie. Nature, 413: 622–625. doi:10.1038/35098065. PMID:11675783.

Ma, Y.C., Piao, S.L., Sun, Z.Z., Lin, X., Wang, T., Yue, C., and Yang, Y. 2014. Stand ages regulate the response of soil respiration to temperature in a Larix principis-ruprechtii plantation. Agric. For. Meteorol. 184: 179–187. doi:10.1016/j.agrformet.2013.10.008.

McClaugherty, C.A., Aber, J.D., and Melillo, J.M. 1984. Decomposition dynamics of fine roots in forested ecosystems. Oikos, 42: 378–386. doi:10.2307/3544408.

McDowell, N.G., Marshall, J.D., Hooker, T.D., and Musselman, R. 2000. Estimating CO2 flux from snowpacks at three sites in the Rocky Mountains. Tree Physiol. 20: 745–753. doi:10.1093/treephys/20.11.745. PMID:12651510.

McMillan, A.M.S., Winston, G.C., and Goulden, M.L. 2008. Age-dependent response of boreal forest to temperature and rainfall variability. Glob. Change Biol. 14: 904–1916. doi:10.1111/j.1365-2486.2008.01614.x.

Minchin, P.E.H., and Lacoitgne, A. 2005. New understanding on phloem physiology and possible consequences for modelling long-distance carbon transport. New Phytol. 166: 771–779. doi:10.1111/j.1469-8137.2005.01323.x. PMID:15869640.

Mkhabela, M.S., Amiro, B.D., Barr, A.G., Black, T.A., Hawthorne, I., Kidston, J., et al. 2009. Comparison of carbon dynamics and water use efficiency following fire and harvesting in Canadian boreal forests. Agric. For. Meteorol. 149: 783–794. doi:10.1016/j.agrformet.2008.10.025.

Natural Regions Committee. 2006. Natural regions and sub-regions of Alberta. Compiled by D.J. Downing, and W.W. Pettapiece. Government of Alberta. Pub. No. T/852. pp. 1–254.

Noormets, A., Chen, J., and Crow, T.R. 2007. Age-dependent changes in ecosystem carbon fluxes in managed forests in northern Wisconsin, USA. Ecosystems, 10: 187–203. doi:10.1007/s10021-007-9018-y.

Peichl, M., Arain, M.A., Ullah, Y., and Moore, T.R. 2010a. Carbon dioxide, methane, and nitrous oxide exchanges in an age-sequence of temperate pine forests. Glob. Change Biol. 16: 2198–2212. doi:10.1111/j.1365-2486.2009.02066.x.

Peichl, M., Brodeur, J.J., Khomik, M., and Arain, M.A. 2010b. Biometric and eddy-covariance based estimates of carbon fluxes in an age-sequence of temperate pine forests. Agric. For. Meteorol. 150: 952–965. doi:10.1016/j.agrformet.2010.03.002.

Phillips, C.L., Nickerson, N., Risk, D., and Bond, B.J. 2011. Interpreting diel hysteresis between soil respiration and temperature. Glob. Change Biol. 17: 515–527. doi:10.1111/j.1365-2486.2010.02250.x.

Pregitzer, K.S., and Euskirchen, E.S. 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. Glob. Change Biol. 10: 2052–2077. doi:10.1111/j.1365-2486.2004.00866.x.

Qi, Y., Xu, M., and Wu, J.G. 2002. Temperature sensitivity of soil respiration and its effects on ecosystem carbon budget: non-linearity begets surprises. Ecol. Model. 153: 131–142. doi:10.1006/soio.2000.100506-3.

Ramirez, K.S., Craine, J.M., and Fierer, N. 2010. Nitrogen fertilization inhibits soil microbial respiration regardless of the form of nitrogen applied. Soil Biol. Biochem. 42: 2336–2338. doi:10.1016/j.soilbio.2010.08.032.

Raymond, M.B., and Jarvis, P.G. 2000. Temporal and spatial variation of soil CO2 efflux in a Canadian boreal forest. Soil Biol. Biochem. 32: 35–45. doi:10.1016/S0038-0717(99)00108-8.

Russell, C.A., and Voroney, R.P. 1998. Carbon dioxide efflux from the floor of a boreal aspen forest. I. Relationship to environmental variables and estimates of C respired. Can. J. Soil Sci. 78: 301–310. doi:10.4141/S97-054.

Ryan, M.G., and Law, B.E. 2005. Interpreting, measuring, and modeling soil respiration, Biogeochemistry, 73: 3–27. doi:10.1007/s10533-004-5167-7.

Saiz, G., Byrne, K.A., Butler-Bahl, K., Kiese, R., Blujdea, V., and Farrell, E.P. 2006. Stand age-related effects on soil respiration in a first rotation Sitka spruce chronosequence in central Ireland. Glob. Change Biol. 12: 1007–1020. doi:10.1111/j.1365-2486.2006.01145.x.

Saurette, D.D., Chang, S.X., and Thomas, B.R. 2006. Some characteristics of soil respiration in hybrid poplar plantations in northern Alberta. Can. J. Soil Sci. 86: 257–268. doi:10.4141/S05-083.

Saurette, D.D., Chang, S.X., and Thomas, B.R. 2008. Autotrophic and heterotrophic respiration rates across a chronosequence of hybrid poplar plantations on northern Alberta. Can. J. Soil Sci. 88: 261–272. doi:10.4141/CJSS07005.

Shi, P.L., Zhang, X.Z., Zhong, Z.M., and Ouyang, H. 2006. Diurnal and seasonal variability of soil CO2 efflux in a cropland ecosystem on the Tibetan Plateau. Agric. For. Meteorol. 137: 220–233. doi:10.1016/j.agrformet.2006.02.008.

Shi, Z. 2010. Afforestation and stand age affected soil respiration and net ecosystem productivity in hybrid poplar plantations in central Alberta, Canada. M.Sc. dissertation, University of Alberta, Canada.

Soil Classification Working Group. 1998. The Canadian system of soil classification. Agriculture and Agri-Food Canada Publication 1646 (Revised).
Tang, J., Bolstad, P.V., and Martin, J.G. 2009. Soil carbon fluxes and stocks in a Great Lakes forest chronosequence. Glob. Change Biol. 15: 145–155. doi:10.1111/j.1365-2486.2008.01741.x.

Tang, J.W., Baldocchi, D.D., and Xu, L. 2005. Tree photosynthesis modulates soil respiration on a diurnal time scale. Glob. Change Biol. 11: 1298–1304. doi:10.1111/j.1365-2486.2005.00978.x.

Tedeschi, V., Rey, A., Manca, G., Valentini, R., Jarvis, P.G., and Borghetti, M. 2006. Soil respiration in a Mediterranean oak forest at different developmental stages after coppicing. Glob. Change Biol. 12: 110–121. doi:10.1111/j.1365-2486.2005.01081.x.

Teklay, T., and Chang, S.X. 2008. Temporal changes in soil carbon and nitrogen storage in a hybrid poplar chronosequence in northern Alberta. Geoderma, 144: 613–619. doi:10.1016/j.geoderma.2008.01.023.

Teklay, T., Shi, Z., Attaeian, B., and Chang, S.X. 2010. Temperature and substrate effects on C & N mineralization and microbial community function of soils from a hybrid poplar chronosequence. Appl. Soil Ecol. 46: 413–421. doi:10.1016/j.apsoil.2010.09.009.

Thuille, A., and Schulze, E.D. 2006. Carbon dynamics in successional and afforested spruce stands in Thuringia and the Alps. Glob. Change Biol. 12: 325–342. doi:10.1111/j.1365-2486.2005.01078.x.

Wang, C.K., Yang, J.Y., and Zhang, Q.Z. 2006. Soil respiration in six temperate forests in China. Glob. Change Biol. 12: 2103–2114. doi:10.1111/j.1365-2486.2006.01234.x.

Wiseman, P.E., and Seiler, J.R. 2004. Soil CO2 efflux across four age classes of plantation loblolly pine (Pinus taeda L.) on the Virginia Piedmont. For. Ecol. Manage. 192: 297–311. doi:10.1016/j.foreco.2004.01.017.

Xu, M., and Qi, Y. 2001. Spatial and seasonal variations of Q(10) determined by soil respiration measurements at a Sierra Nevadan forest. Glob. Biogeochem. Cycles, 15: 687–696. doi:10.1029/2000GB001365.

Yan, J.H., Wang, Y.P., Zhou, G.Y., and Zhang, D.Q. 2006. Estimates of soil respiration and net primary production of three forests at different succession stages in South China. Glob. Change Biol. 12: 810–821. doi:10.1111/j.1365-2486.2006.01141.x.

Yemshanov, D., Biggs, J., McKenney, D.W., and Lempriere, T. 2012. Effects of permanence requirements on afforestation choices for carbon sequestration for Ontario, Canada. Forest Policy Econ. 14: 6–18. doi:10.1016/j.forpol.2011.08.010.

Zha, T., Barr, A.G., Black, T.A., McCaughey, J.H., Bhatti, J., and Hawthorne, I., 2009. Carbon sequestration in boreal jack pine stands following harvesting. Glob. Change Biol. 15: 1475–1487. doi:10.1111/j.1365-2486.2008.01817.x.