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Afforestation and stand age affected soil respiration and net ecosystem productivity in hybrid poplar plantations in central Alberta, Canada

by

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Abstract

Afforestation and stand development can significantly affect soil respiration and net ecosystem productivity (NEP). I studied 1) the effects of afforestation on NEP by comparing cropland previously planted to barley (on a barley-barley-alfalfa-alfalfa-alfalfa rotation) and that converted to a hybrid poplar (*Populus deltoides* × *Populus* × *petrowskyana* var. Walker) plantation and 2) the NEP along a chronosequence of stands aged 5-, 8-, 14-, and 16-year old in 2009 in central Alberta, Canada. Soil respiration and NEP decreased in the first two to three years after afforestation, while both generally increased with stand development. The *ecosys* model was used to simulate carbon dynamics in the plantations over a 20-year rotation under contrasting soil conditions. Soil conditions of the 14-year-old plantation accumulated the greatest amount of ecosystem carbon over the whole rotation. The research indicated that plantations could be a net carbon source in the first few years after afforestation and then became a net carbon sink, helping to mitigate net CO_2 emissions for the remainder of the rotation.

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Chapter 1 Introduction

Introduction

Climate warming is unequivocally based on the observed rise in global average air and ocean temperatures, and the increased rate of the warming of global surface temperature over the last 50 years (1956 – 2005), of 0.13 °C per decade, is nearly twice that recorded for the past 100 years (1906 – 2005), with 0.074 °C per decade (IPCC 2007). Changes in the atmospheric concentrations of greenhouse gases (GHG) alter the energy balance of climate systems and are ones of the drivers of climate warming (IPCC 2007). Global GHG emissions have been increasing since pre-industrial times due to human activities, with an increase of 70% from 1970 to 2004 (IPCC 2007). The most important anthropogenic GHG, CO_2 concentration has increased from 280 ppm (pre-industrial value) to 379 ppm in 2005, mainly due to fossil fuel combustion and land use changes (Vitousek et al. 1997, Schimel et al. 2001, IPCC 2007).

Land use changes can cause dramatic changes in carbon storage in both soil organic matter and plant biomass. Land use changes, in particularly deforestation, resulted in the release of 100 Pg C to the atmosphere over 130 years from 1850 to 1980 (Houghton 1995), 124 Pg C from 1850 to 1990 (Houghton 1999), and 1.6 Pg C yr^{-1} over ten years during 1980 – 1989 (Dixon et al. 1994), significantly altering ecosystem carbon cycling in terrestrial ecosystem. About 0.2 Pg C yr^{-1} was lost from 1989 to 1998 due to deforestation and abandonment of agricultural lands in the Brazilian Amazon (Houghton et al. 2000). The conversion of forest to agricultural lands is one type of land use change which has been ongoing over the last several decades, resulting in approximately 800 x 10^6 ha of forest being cleared for agricultural uses and 2000 x 10^6 ha being harvested for fibre (Houghton 1999, Richter et al. 1999). In boreal regions, 44% of soil carbon losses were observed after boreal forests, mainly aspen (*Populus tremuloides* Michx.), spruce (*Picea glauca* Voss), and willow (*Salix alba* sp.), were converted to agricultural land use over a 20-year period (Grunzweig et al. 2003). Through a meta-analysis, Guo and Gifford (2002a) found that 42% of the soil carbon was lost by converting native forests to crop lands. Loss of soil organic carbon (SOC) could amount to 50% of the C in the surface soils (20 cm) after cultivation for 30 – 50 years, and 30% in the top 100 cm over the same time period (Post and Kwon 2000). The rapid decline in SOC could be because cultivation of the cropland breaks up soil aggregates, exposes the SOC from the deep soil to the ambient environment, and therefore causes a substantial loss of soil carbon. For example, 78 ± 12 Gt carbon was lost due to short-sighted farming practices, e.g., ploughing which turns over the soil and makes soil organic carbon susceptible to decomposition (Lal et al. 2004). Even if the productivity of the newly established cropland is the same as the previous forest, it would not fully recover the lost soil carbon, because most of the agricultural productivity is harvested and respired thereafter.

However, land use changes, such as afforestation or re-growth of forests on abandoned agricultural lands could increase the carbon sink of terrestrial ecosystems (Schimel et al. 2001), in both soil and vegetation carbon stocks, especially for the recovery of SOC lost during the agricultural land use period. Therefore, afforestation has been considered as an effective method to mitigate net CO_2 emissions (IPCC 2001, Jandl et al. 2007). In a review by Post and Kwon (2000) on land use change effects on soil carbon sequestration, the average soil carbon accumulation rates were 33.8 g C m^{-2} yr^{-1} for forest after conversion from the abandoned agricultural lands. Guo and Gifford

(2002a) found that soil carbon increased by 18 and 53% when croplands were converted to plantations and secondary forests, respectively. Generally, after establishment of forests or plantations, high input rates and low decomposition rates of organic matter could favour carbon sequestration in the soils. In a review by Paul et al. (2002) on soil carbon changes following afforestation, they concluded that after afforestation, soil carbon in the 0-10 cm soil layer decreased by 3.46% per year for the first five years and recovered to the initial carbon content by age 30. After age 30, soil carbon stayed constant in the same soil layer, while increasing by between 0.50 and 0.86% per year at the other depths (> 10 cm or > 30 cm). The decrease in soil carbon content over the first five years was attributed to the low carbon input and high rate of soil carbon mineralization. Changes in soil carbon content after afforestation can also be affected by forest type (Paul et al. 2002, Laganiere et al. 2009) due to variation in the quality of carbon inputs, plant productivity, rooting pattern etc. For example, Morris et al. (2007) found that deciduous and coniferous forests (average age was about 50 years) established on agricultural soils accumulated 0.35 and 0.26 Mg C ha^{-1} yr^{-1}, respectively, as compared to the adjacent agricultural land in southwest Michigan. However, Richter et al. (1999) observed that soil carbon hardly increased after reestablishment of pine forests over 40 years, with strong carbon sinks in tree biomass and litterfall. Apart from the forest type effect on soil carbon accumulation, Laganiere et al. (2009) concluded that another four main factors, land use history, soil clay content, preplanting disturbance and climatic zone, could also affect soil carbon sequestration after afforestation. Taking the soil clay content effect on SOC as an example, in the review by Laganiere et al. (2009) they found that soils with high clay contents sequestered more SOC than soils with low clay contents after afforestation. They attributed this result to more physical protection of clay particles to the SOC from decomposition by forming a stable organo-clay complex.

Quantifying the carbon storage in a forest is necessary for estimating rates of carbon sequestration and for assessing the role of forests in offsetting net CO_2 emissions (Curtis et al. 2002). After afforestation, the carbon balance of a forest ecosystem changes with forest development (Litvak et al. 2003a, Kolari et al. 2004, Grant et al. 2007b, Zha et al. 2009). Net ecosystem productivity (NEP) has been extensively used as an index to represent the carbon balance of a forest during a certain period of time (Bond-Lamberty et al. 2004b, Howard et al. 2004, Arain and Restrepo-Coupe 2005, Arevalo et al. 2009, Zha et al. 2009). The NEP is the difference between CO_2 input via photosynthesis and output through ecosystem respiration, and also can be considered as the balance between net primary productivity (NPP) and heterotrophic respiration (R_h). Stand age is a significant source of variability in NEP (Pregitzer and Euskirchen 2004). The variation in NEP along a chronosequence of a forest ecosystem represents the changes in carbon balance as the forest grows. In the initial years after a forest plantation is established or recovered from some form of disturbance, heterotrophic respiration from the decomposition of residues and soil organic matter is typically greater than CO_2 uptake by photosynthesis (Grant et al. 2007a), and thus the plantations would act as a carbon source at that stage. With forest development, NPP increases rapidly due to greater photosynthetic capacity of the trees and R_h decreases because of the depletion of easily decomposable substrates and reduced fresh carbon supply (Grant et al. 2007b). Now forest stands might turn into C sinks. As forest stands mature, NPP declines due to decreased soil nutrient availability, increased stomatal limitation, or a rise in respiring tissue (Gower et al. 1996), the forests might become a smaller C sink, C neutral or even become a C source again.

Much research has been conducted on how NEP changes with stand age in natural (Litvak et al. 2003a, Howard et al. 2004, Humphreys et al. 2006, Thuille and Schulze 2006, Zha et al. 2009) or managed forests (Noormets et al. 2007, Yang et al. 2007, Black et al. 2009, Karu et al. 2009). Litvak et al. (2003a) observed that NEP in five boreal black spruce stands increased with stand age (11, 19 and 36 years old) and then decreased with stand age (70 and 130 years old). Howard et al. (2004) found that NEP increased with stand age (0, 5, 10, and 29 years old) and decreased at 79 years old in a boreal jack pine forest. In a review of Pregitzer and Euskirchen (2004) on biome patterns related to forest age, based on five age classes (A: 0 - 30, B: 31 - 70, C: 71 - 120, D: 121 - 200, E: > 200), they synthesized that NEP increased from age class A to B, decreased from B to C, and then levelled out from C to E in temperate forests, and that NEP increased from age class A to C, decreased from C to D, and then levelled out from D to E in boreal forests. Pregitzer and Euskirchen (2004) also pointed out that the great variability of NEP could be attributed to the stand age rather than the inter-annual change of climate. In a chronosequence (3, 6, 12, 20, 37, 71, and 151 years old) study of a boreal black spruce on NEP by Bond-Lamberty et al. (2004b), NEP increased from carbon sources in the young stands (3, 6, and 12 years old), to large sinks in the middle-age stands (20, 37 and 71 years old), and became carbon neutral in the old stand (151 years old). Noormets et al. (2007) found that NEP over the growing season increased from 3-year-old clear-cuts to the mature stand (65 years old) in managed forests in northern Wisconsin, USA, with all stands being carbon sinks except for the 3-year-old clear-cut. In four different aged (2, 10, 29, and 90 years old) boreal jack pine stands, Zha et al. (2009) found that the annual mean NEP increased with stand age from a carbon source in a 2-year-old stand to a moderate carbon sink in the 29-year-old stand, and declined to a weak carbon sink in the 90-year-old stand. Zha et al. (2009) proposed that the time course variability of NEP could probably originate from stand age due to changes in leaf area index. Grant et al. (2007a) used the ecosystem model *ecosys* to simulate the stand age effect on boreal jack pine stands from clear-cutting and successfully modelled the increase in NEP with stand age until stands matured, and then gradually declined afterwards due to a decrease in stem axial conductance associated with an increase in bole height.

Soil respiration, which includes root respiration and heterotrophic respiration, is a major contributor to the forest carbon balance (Ryan and Law 2005, Gaumont-Guay et al. 2009) and often dominate ecosystem respiration (Valentini et al. 2000). Afforestation has also been shown to have a significant influence on soil respiration (Raich and Tufekcioglu 2000, Campos 2006, Saurette et al. 2008a, Shi et al. 2009, Arevalo et al. 2010, Sheng et al. 2010). In a review by Raich and Tufekcioglu (2000) on the relationship between vegetation and soil respiration, no significant difference in soil respiration was observed between cropland and adjacent forest. Raich and Tufekcioglu (2000) attributed the non-significance in soil respiration to the large variety of crops and cropping systems included in their review. Saurette et al. (2008a) found no effects on soil CO_2 emission in the first year after afforestation from barley to Walker poplar (*Populus deltoides* × *Populus* × *petrowskyana* var. Walker) in the boreal region of central Alberta, Canada. Arevalo et al. (2010) also studied land use change effects on soil respiration in the same ecoregion in 2006, and they found that the average cumulative soil respiration over two growing seasons in the agriculture land was greater than that in the 2-year-old Walker poplar plantation in a pseudoreplicated experiment. Sheng et al. (2010) showed that soil respiration decreased by 50% in natural forests converted to slope tillage in southern China and argued that the decline in soil respiration from a natural forest to slope tillage was probably caused by the lower carbon substrate input from slope tillage than from the natural forest.

Stand age also has a great influence in soil respiration (Bond-Lamberty et al. 2004b, Wiseman and Seiler 2004, Saiz et al. 2006, Saurette et al. 2006, 2008b). Saurette et al. (2006) found that soil respiration increased with stand age in three different aged hybrid poplar plantations established on previously agricultural lands in the boreal forest ecological region. Similarly Arevalo et al. (2010) observed that soil respiration in a 9-year-old hybrid poplar plantation was greater than that in a 2-year-old hybrid poplar plantation in northern Alberta, both of which were established on previously cleared agricultural lands. They argued that substrate input and root biomass increased with stand age and therefore caused a stand age effect on soil respiration. However, Tedeschi et al. (2006) found that soil respiration decreased with stand age in coppiced oak, in central Italy (Chronosequence: 1, 5, 10 and 17 years old). They postulated that the decrease in soil respiration was caused by the shift in the distribution of the respiratory substrate. A similar result was found by Saiz et al. (2006) where soil respiration decreased with stand age until 31 years-old and then leveled out in the older stands (Chronosequence: 10, 15, 31, and 41 years old) in a first rotation Sitka spruce stand in central Ireland. Saiz et al. (2006) hypothesized that higher productivity might cause lower soil respiration in a given ecosystem and exert a confounding effect on the influence of stand age on soil respiration. Other different results were also found by Tang et al. (2009) in a chronosequence (0, 10, 26, 73 and 350 years old) of deciduous forests in Wisconsin and Michigan where cumulative soil respiration increased with stand age, peaked at intermediate age (26 years old) and then declined as the stand got older. Tang et al. (2009) found that root biomass could most likely cause the age effect on soil respiration due to its similar stand age pattern to soil respiration. In a boreal black spruce chronosequence, Bond-Lamberty et al. (2004a) found soil respiration generally increased with stand age from 4 to 21 years old, except for a 7 year-old stand which had the smallest respiration, and decreased from 21 to 152 years old. Similarly, soil respiration increased in aspen stands from 24-27 years old to 42-48 years old, but decreased from 67-72 years old in mature northern hardwood stands (Bolstad et al. 2004).

There is a growing interest in planting highly productive, intensively grown plantations such as with short rotation hybrid poplar on marginal agricultural lands in Canada to supply fibre to the pulp and paper industry (Samson et al. 1999a). Meanwhile, this productive forestry can sequester greater CO_2 from the atmosphere mainly due to their faster rate of growth compared with native forests in the region. In Canada, the provincial government of Saskatchewan announced plans to convert 1.62 million hectares of agricultural land into tree plantations over the next 20 years by mainly planting hybrid poplars (Haverstock 2005a). In our research site, Alberta-Pacific Forest Industries Inc. (Al-Pac) has leased and planted approximately 1200 hectares of marginal agricultural land per year in north-central Alberta with the goal of planting 25 000 hectares of land into hybrid poplar plantations by the year 2020 (http://www.alpac.ca/index.cfm?id=poplarfarming). In British Columbia and Ontario, a sophisticated system for planting and breeding hybrid poplars has been developed over decades (Welham et al. 2007). Planting these short-rotation woody crops even has political and economic impacts, since countries may choose to account for forest management activities to fulfill their commitments under the Kyoto Protocol (Bernstein 2002a). Until now, little research has attempted to verify C accumulation of these hybrid poplar plantations established by forest companies such as Al-Pac which should be an important part of evaluating C accumulation in Canada.

The lack of a replicated chronosequence of field data in these hybrid poplar plantations has resulted in the development of conceptual and mathematical models to project the long-term carbon storage over varying rotation lengths. A given ecosystem model, *ecosys*, is applicable and allows us to project net primary productivity and net ecosystem productivity over a whole forest rotation to provide the entire verifiable C value (Grant and Nalder 2000, Grant et al. 2003, Grant et al. 2007b, Grant et al. 2009a). *Ecosys* has been successfully applied to many native forests, especially boreal forests and even tundra soils to simulate net primary productivity and ecosystem productivity under many different climate scenarios e.g. drought and warming (Grant et al. 1999, Grant et al. 2001, Grant et al. 2003, Grant et al. 2005, Grant et al. 2007b, Grant et al. 2009a), but it has not been used previously for simulation in managed plantations with short rotations, such as with hybrid poplar plantations.

Even though plenty of research has been done on how NEP and soil respiration respond to land use changes and forest age, many of these studies were focused on long-term effects (Poulton et al. 2003, DeGryze et al. 2004, Saiz et al. 2006, Tedeschi et al. 2006, Morris et al. 2007, Tang et al. 2009a). The short-term land use change and stand age effects on NEP and soil respiration have been less studied (Post and Kwon 2000, Saurette et al. 2006, Saurette et al. 2008a, Saurette et al. 2008b, Arevalo et al. 2010). In addition, less information is currently available for the changes in annual NEP in hybrid poplar plantations over the whole rotation after establishment on agricultural lands.

This thesis includes five chapters. Chapter 1 (this chapter) provides the introduction to the whole research project. Chapter 2 examines the afforestation effect on soil respiration and NEP in boreal Alberta. Chapter 3 addresses the effect of stand age on soil respiration and NEP in several hybrid poplar plantations. Chapter 4 is the modelling of carbon accumulation in the different aged hybrid poplar plantations. Chapter 5 presents conclusions and synthesis of the research project.

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Chapter 2 Afforestation impacts on soil respiration, temperature sensitivity and net ecosystem productivity in central Alberta

1. Introduction

Globally the soil contains an enormous amount of carbon (2500 Gt) in both organic and inorganic forms. The soil carbon pool is more than three times as large as the atmospheric carbon pool and five times larger than that of the biotic pool, i.e., the vegetation (Lal 2004). Therefore, even a slight change of the soil carbon pool could significantly affect the atmospheric carbon dioxide concentration. One of the factors that can cause significant changes in soil carbon storage is land use change, which could have a major impact on soil carbon dynamics (Dixon et al. 1994, Raich and Tufekcioglu 2000, DeGryze et al. 2004, Laganiere et al. 2009). Land use change is one of the drivers of the global carbon cycle. It is critical therefore to understand the effects of land use change on soil carbon stocks, in the context of “international policy agendas” on the mitigation of greenhouse gas emissions (Guo and Gifford 2002). We recognize that land use change can occur in many different ways such as deforestation to change forests to agricultural production and the reverse is called afforestation when planting of trees occurs on agricultural land that has been in agricultural use for the last 50 years.

In previous studies, researchers have found that land use changes, mostly deforestation, resulted in the release of 100 Pg C to the atmosphere over 130 years from 1850 to 1980 (Houghton 1995) and 1.6 Pg C yr^{-1} over nine years during 1980 – 1989 (Dixon et al. 1994). However, afforestation of agricultural lands can increase ecosystem C storage, in the forms of soil and plant biomass C (Guo and Gifford 2002, Poulton et al.

2003, Morris et al. 2007). For example, Morris et al. (2007) found that deciduous and coniferous forests (average age was about 50 years) established on agricultural soils accumulated in soil carbon by 0.35 and 0.26 Mg C ha^{-1} yr^{-1}, respectively, as compared to the adjacent agricultural land in southwest Michigan. With the growing interest of establishing short-rotation plantations, such as hybrid poplar, afforestation is considered an effective way to mitigate net CO_2 emissions (FAO 2004). Afforestation can be a source for fibre, timber or biomass energy (Samson et al. 1999). Biomass energy can be used as a substitute for fossil fuels to decrease global fossil fuel consumption by up to 20% (Detwiler and Hall 1988) while accumulation of C in the detritus will directly contribute to the reduction of CO_2 concentrations in the atmosphere. Therefore, it is very important to fully understand the effects of afforestation on ecosystem carbon budgets.

Changes in soil carbon stocks are determined by the difference between carbon inputs (mainly leaf and root litter) and outputs mainly in the form of soil organic matter decomposition (Shi et al. 2009). Soil respiration is a major pathway of soil organic carbon output and shows a great deal of diurnal and seasonal variability (Fang et al. 1998, Xu and Qi 2001a, Gaumont-Guay et al. 2006, Wang et al. 2006). Therefore, it is crucial to understand these variations and the controlling factors in different land uses, in order to better understand and accurately model soil carbon dynamics. In addition, temperature sensitivity of soil respiration has been found to vary among different land uses (Grunzweig et al. 2003, Arevalo et al. 2010, Sheng et al. 2010), and knowing the temperature sensitivity of soil respiration in different land uses has profound implications for the global carbon cycle. For example, in Arevalo et al. (2010) the temperature sensitivity of soil respiration in agricultural land was found to be greater than that in the

2- and 9-year-old hybrid poplar plantations, and grassland and a native aspen forest had the lowest temperature sensitivity in the boreal ecoregion of northern Alberta.

Even though plenty of research has been done on land use change effects on soil carbon stocks, many of them studied long-term effects of land use changes (Poulton et al. 2003, DeGryze et al. 2004, Morris et al. 2007). The short-term land use change effects on soil carbon stocks have been less studied (Post and Kwon 2000, Saurette et al. 2008a, Arevalo et al. 2010). In the initial years after plantations were established on agricultural lands, the former soil carbon equilibrium would be broken and the newly established plantation would be starting to lose soil carbon rapidly due to disturbance until a new equilibrium is reached. Therefore, it is crucial to capture the short-term dynamics of soil carbon. Saurette et al. (2008a) found no effects on CO_2 emission in 2006 in the first year after land use change from barley to Walker poplar (*Populus deltoides* × *Populus* × *petrowskyana* var. Walker) in the same study site. However, Saurette et al. (2008) only studied soil CO_2 emission for the first year after afforestation, which is also very important in capturing the variation in soil CO_2 emissions in the two different land uses. Saurette et al. (2008) used a static chamber system to measure soil respiration, which only provided soil respiration measurements once every two weeks, and thus the poor temporal resolution could not capture the response of soil respiration to individual precipitation events or the diurnal variation of soil respiration (Savage and Davidson 2003). Arevalo et al. (2010) also studied land use change effects on soil respiration in the same ecoregion in 2006, and found that the average cumulative soil respiration over two growing seasons in the agriculture land was greater than that in the 2-year-old Walker poplar plantation in a pseudo-replicated experiment.

In the current study, we used an automated chamber system (ACS) to measure soil respiration every two hours, allowing us to capture the short-term response of soil respiration to rainfall events for accurate estimation of soil respiration and diurnal variations. The questions studied in this project were: 1) does soil respiration increase or decrease after land use change from cropland to hybrid poplar plantations? 2) what are the diurnal and seasonal variations in soil respiration, and what are the controlling factors for soil respiration in the two different land uses? and 3) does land use change affect the temperature sensitivity of soil respiration?

2. Methods

2.1. Site description

The study site was located near Alberta-Pacific Forest Industries Inc. (Al-Pac) mill site (54°49′N, 113°31′W), in the southern area of the Boreal Mixedwood ecological subregion in northern Alberta, Canada. The climate in this area is continental, with short, warm summers and long, cold winters. The growing season is about 175 to 180 days, from May to October (Government of Alberta 2006). Mean annual temperature and precipitation in this area are 2.1 °C and 503.7 mm (including snow fall, Environment Canada 2004), respectively. Aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* Voss), and jack pine (*Pinus banksiana* Lamb) are the dominant native tree species on uplands in this area (Natural Regions Committee, 2006). The primary landform is level to gently undulating plains and the dominant soil type based on the Canadian system of soil classification (Soil Classification Working Group 1998) is Gray Luvisol, with Dystric and Eutric Brunisols occurring in areas with coarse textured soils (Natural Regions Committee 2006). The experimental area occurs on Gleysolic soil according to Saurette et al. (2008a). This research area had been used for agriculture activities for the latter half of the twentieth century.

2.2. Experimental design

A completely randomized block design was used to conduct the study with three blocks and two treatments: alfalfa (*Medicago sativa* L.) and Walker poplar (*Populus deltoides* × *Populus* × *petrowskyana* var. Walker), with a total of six plots established. All plots were seeded to barley (*Hordeum vulgare* L.) in summer 2004 and harvested in September 2004. In spring 2005, all plots were disced in preparation for planting and seeding. The agricultural plots were again seeded to barley in July 2005 and harvested in September, and the other three plots were planted to Walker poplar in June 2005. Walker poplar trees were planted using over-winter dormant stock at a spacing of 3 x 3 m or 1111 stems/ha. In spring 2006, the plots previously planted to barley were converted to alfalfa. Alfalfa was harvested in July and September, twice a year in 2006, 2007 and 2008. The Walker plots were disced in between the tree rows in the summer from 2005 to 2008 to control weeds. Soil characteristics were described in Appendix I and Saurette et al. (2008).

2.3 Soil respiration measurement

Soil respiration was measured using a non-steady state automated chamber system (ACS) from June to early October, 2007 and from June to early November, 2008. Each ACS unit was equipped with three transparent chambers (52.5 cm internal diameter, 50 L or 0.05

m^3 in volume). The lid for the chamber was dome-shaped. The system was programmed such that the three chambers would close sequentially for one minute every two hours. When a chamber was closed, the air in that chamber was kept pumping into an infrared gas analyzer (IRGA) housed in a white metal box. The CO_2 concentration was determined by the IRGA (LI810 CO_2/H_2O analyzer) every second for one minute. The slope of the CO_2 concentration increase was derived using linear regression. Soil respiration (R_s) was calculated using the following equation:

$$\mathbf{R_s = \rho_a \frac{V}{A}\frac{ds_c}{dt}}$$

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), ds_c/dt is the rate of change of the CO_2 mixing ratio in the headspace over the measurement time. The lids were kept open when the chambers were not in use to allow rain and litter to fall into the collar area to maintain the condition inside the chamber as close to natural as possible. Two ACS with six chambers were installed in the land use trial, with one chamber installed in each experimental plot. The ACS had a microcomputer to control the operation of the system and power was supplied through two deep cycle marine batteries (12V, EHP advance generation, Duracell), linked to a solar panel (85w, BP585U, bpsolar) that charged the batteries.

Approximately 15% of the soil respiration data were lost across the treatments due to insufficient power supply in rainy/cloudy days or improper closure of the chambers. Data for the night-time in 2007 and daily data in 2008 with acceptable slopes (the coefficient of determination greater than 80%) of increased CO_2 concentration during the one minute measurement period were retained for further analysis. Data for the daytime in 2007 were kept only if the night-time slope for CO_2 concentration change during the one-minute measurement time was not flat. When flat slopes occurred at night, which meant the chamber was not properly closed, and then the daytime data with flat slopes were not used in the following data analysis.

In 2007, understory vegetation was allowed to grow in the measurement chambers. Soil respiration measured in the daytime was therefore CO_2 efflux from soil reduced by photosynthetic uptake of understory vegetation in the chambers. In 2008, the transparent lids of the measurement chambers were covered with an inner layer of dark paper and an outer layer of aluminum foil and aboveground understory vegetation in the chambers was cut to ground level every two weeks. Thus the confounding effect of photosynthesis by understory vegetation on CO_2 concentration inside the chambers during the measurement period was removed.

2.4. Soil temperature and soil water content measurement

Soil temperature was measured every two hours at 5 cm below the soil surface with a copper-constantan thermocouple (Omega Engineering, Montreal, QC) located near the chambers and the data was stored in the microcomputer that controlled the ACS. Soil temperature at 10, 20, 30 and 40 cm depths was measured every hour with copper-constantan thermocouples and data-logged with Campbell Scientific CR10X dataloggers (Campbell Scientific, Inc., Logan, UT). Volumetric water content at 10 and 20 cm depth was measured every hour using Campbell Scientific CS616 water content reflectometers (Campbell Scientific, Inc., Logan, UT) and datalogged with a CR10X datalogger.

2.5. Calculations on temperature sensitivity of soil respiration (Q_{s10})

Soil respiration and soil temperature were fit into the Q_{s10} model:

$$R_s = R_{s10}\, Q_{s10}^{\,(Ts-10)/10}$$

where R_s is the daily mean soil respiration rate (µmol m^{-2} s^{-1}), R_{s10} is the soil respiration rate at 10 °C, Q_{s10} is the temperature sensitivity of soil respiration, which is defined as the relative increase in soil respiration for a 10°C increase in soil temperature, and T_s is the daily mean soil temperature (°C). Short-term Q_{s10} was calculated using soil temperature at 5 cm depth, because soil temperature at 5 cm depth would be more closely associated with short-term Q_{s10}.

2.6. Heterotrophic (Rhs) and total soil respiration (Rt)

In order to separate total soil respiration into heterotrophic and autotrophic respiration, a 15 cm diameter polyvinyl chloride cylinder was inserted into the soil to a 50 cm depth to cut off the roots of the vegetation on site in 2008. Soil respiration inside and outside the cylinder was measured using a static chamber system. Soil respiration measured inside the cylinder was heterotrophic respiration (Rhs) and outside the cylinder was total soil respiration (Rt). At each measurement, a 20 mL air sample in the static chamber was taken at 0, 5, and 10 minutes and injected into a pre- evacuated exutainer. The CO_2 concentration was measured on a Varian CP-3800 gas chromatograph (Varian Canada, Mississauga, Canada). The Rt and Rhs were calculated based on the changes in CO_2 concentration during the sampling intervals. See Saurette et al. (2008a) for a detailed description of the method for calculating Rt. The Rhs:Rt ratio was calculated to determine heterotrophic respiration over the growing season using the following equation.

$R_h = R_s$ * (Rhs: Rt)

Where R_h is heterotrophic respiration over the growing season, R_s is soil respiration over the growing season measured by the automated chamber system.

2.7. Net primary productivity and net ecosystem productivity

Tree height (H) and diameter at breast height (DBH) were measured at the beginning and end of the 2008 growing season. Only 300 out of 1050 trees survived from 2005 to 2008, which gave a survival rate of 29%. Tree height and DBH were fit into the following localized biometric equations established by Saurette et al. (in preparation) for oven-dried above- and below-ground biomass of Walker poplars:

$$Aboveground\ Biomass(kg) = 0.6298 * DBH^{1.3582} * H^{0.2353}$$

$$Belowground\ Biomass(kg) = 1.1810 * DBH^{2.5123} * H^{-2.1616}$$

Five 0.5 x 0.5 m quadrants were used to randomly determine above-ground biomass of the alfalfa prior to harvest per treatment plot. The samples were taken into the lab and oven-dried at 65°C until constant weight. The root biomass was determined using a shoot:root ratio of 0.87 developed for alfalfa in eastern Canada (Bolinder et al. 2002).

The biomass in the quadrant was scaled up to a hectare. Alfalfa was harvested twice in 2008 (July and October).

The carbon content of aboveground and belowground was calculated by multiplying a standard factor of 0.5 (Pregitzer and Euskirchen 2004). The net primary productivity (NPP) equaled the biomass carbon increment from the beginning to the end of the growing season. The net ecosystem productivity (NEP) was the carbon increment of the whole ecosystem: NEP = NPP – R_h.

2.8. Data analysis

The difference in soil temperature, soil water content and soil respiration between alfalfa and Walker plots over the two years was tested using repeated measures ANOVA at a significance level $\alpha = 0.05$ in SAS 9.0 (Version 9.0, SAS Institute Inc.), considering day as repeated measures. The normality and homogeneity of variance of treatments in each day were also tested using univariate and levene tests, respectively, in SAS 9.0. No violation of normality of distribution and homogeneity of variance was found. Linear or nonlinear curve fitting was done in Origin (Version 8.0, OriginLab Corp.).

The statistical model for repeated measures ANOVA was:

$$Y_{ijk} = \mu + B_i + T_j + \varepsilon_{ij} + D_k + TD_{ik} + \varepsilon_{ijk}$$

Where:

Y_{ijk} = a dependant variable (soil respiration, soil temperature or soil water content)

μ = overall mean

B_i = the ith block (1, 2, 3) (random factor)

T_j = the jth treatment (Walker, alfalfa) (fixed factor)

ε_{ij} = error main associated with the treatment * block interaction

D_k = the kth day (fixed factor)

TD = the interaction of treatment * day

ε_{ijk} = random error associated with the day * block + day * block * treatment interactions

The difference in short-term soil respiration at 10°C and temperature sensitivity between land uses and months were tested using a two-way ANOVA. Tukey test was performed to separate the means.

3. Results

3.1. Soil temperature and soil water content

Soil temperature (T_s) at 10 cm depth was greater in the Walker than in the alfalfa plots from June to November in both 2007 and 2008 (Fig. 2-1a, 2-1b), and showed a similar trend at the other depths to that at 10 cm for each treatment (data not shown). The T_s in both land uses had a similar seasonal trend in 2007 and 2008 (Fig. 2-1a, 2-1b), and increased from June, reached maximum in mid July in 2007, with 17.3 and 19.2 °C in the alfalfa and Walker plots, respectively, or in mid August in 2008, with 16.9 and 16.2 °C, respectively, and then declined until the end of the measurement period (Fig. 2-1a, 2-1b). No difference in soil water content at 10 cm was observed between the Walker and alfalfa plots throughout the growing season in either year (Fig. 2-1c, 2-1d). Soil water content at 20 cm depth had a similar trend to that at 10 cm depth for each treatment (data not shown).

3.2. Seasonal variation of soil respiration

There was no difference in soil respiration (R_s) between the alfalfa and Walker plots in 2007 (Fig. 2-2a), while a difference ($P < 0.01$) between the two was found in 2008 (Fig. 2-2b). Similar seasonal variation of R_s in both land uses and years were observed during the study. The R_s increased from June, reached a maximum in mid July (2007) or mid August (2008), and then declined until the end of the measurement period (Fig. 2-2). In addition, a small peak in R_s appeared in mid September in both years (Fig. 2-2) and another one occurred in early October in 2008 (Fig. 2-2b).

An exponential relationship between daily mean night-time R_s (R_{sn}) and T_s (T_{sn}) at 10 cm was observed in both land uses in 2007 and 2008 (Fig. 2-3). The relationship fitted well to the Q_{10} model. The T_{sn} at 10 cm explained more variance in R_{sn} in 2008 than in 2007 (75% vs. 37% in alfalfa plots; 72% vs. 22% in Walker plots). Night-time R_{s10} (R_{s10n}) and Q_{s10} (Q_{s10n}) values in the alfalfa plots were higher than those in the Walker plots in both 2007 and 2008 (Fig. 2-3). These two values were greater in 2008 than in 2007 in both alfalfa and Walker plots.

This exponential relationship was also found between daily mean R_s and T_s at 10 cm in both land uses in 2008 (Fig. 2-4). The T_s at 10 cm explained more than 80% of the seasonal variation in daily mean R_s. The daily R_{s10} and Q_{s10} were both greater in the alfalfa than in the Walker plots. Such a relationship between daily mean R_s and T_s was not found in 2007 (data not shown).

The R_{s10n} and Q_{s10n} were determined for each month and were named short-term night-time R_{s10} ($R_{s10n'}$) and Q_{s10} ($Q_{s10n'}$) (Table 2-1). No significant difference in $R_{s10n'}$

was found between the alfalfa and Walker plots in any month in 2007. The $Q_{s10n'}$ in the alfalfa plots was greater than that in the Walker plots, while month had no effect on $Q_{s10n'}$ in 2007. In addition, no land use and month interaction was observed. In 2008, the $R_{s10n'}$ in the alfalfa plots was greater than that in the Walker plots, and $R_{s10n'}$ in June and October were smaller than those in July, August and September. No land use and month interaction was observed on $R_{s10n'}$. The $Q_{s10n'}$ in the Walker plots was greater than that in the alfalfa plots. No effect of month on $Q_{s10n'}$ was found in either the alfalfa or Walker plots.

A linear relationship between daily mean R_s and daily ΔT_s (daily soil temperature difference between the maximum and minimum temperatures) was found in both land uses in 2008 (Fig. 2-5). The ΔT_s explained 41 and 45% of the seasonal variation in R_s in the alfalfa and Walker plots, respectively. Such relationships were not observed in either of the land uses in 2007 (data not shown).

3.3. Diurnal variation of soil respiration

In 2007, similar diurnal variations of R_s were found in the two land uses during the early, mid and late growing seasons. Soil respiration peaked around 02:00 h and reached a minimum around 12:00 h, which were about 6 h and 2 h, respectively, later than those of T_s at 10 cm (Fig. 2-6).

In 2008, similar diurnal variation of R_s was also observed in both land uses during the early, mid and late growing season. Soil respiration peaked around 24:00 h, the same pace with T_s at 10 cm and reached a minimum around 08:00 h, about 4 h earlier than that of T_s at 10 cm (Fig. 2-7).

Hysteresis was found between bihourly soil respiration rates and soil temperature in both land uses. For example, R_s in the cooling part of the day was always higher than that in the warming part of the day with the same temperature in both land uses in June 2008, when soil temperature at 5 cm was used (Fig. 2-8a, 2-8b). However, the inversion of this hysteresis occurred when soil temperature at 10 cm was used in both land uses in 2008 (Fig. 2-8c, 2-8d). Soil respiration at the same soil temperature was greater during the warming part than during the cooling part.

3.4. Land use effect on net ecosystem productivity (NEP)

The NPP and R_h over the growing season were greater in the alfalfa plots than in the Walker plots (NPP: 3.01 vs. 0.10 Mg C ha^{-1}; R_h: 2.11 vs. 1.33 Mg C ha^{-1}) in 2008 (Fig. 2-9). The NEP was 0.9 Mg C ha^{-1} in the alfalfa plots and -1.23 Mg C ha^{-1} in the Walker plots.

4. Discussion

4.1. Land use effects on soil respiration and net ecosystem productivity

Afforestation (converting cropland to Walker poplar plantation) resulted in a significant decrease in soil respiration four years (in a barley-barley-alfalfa-alfalfa crop rotation) after land use conversion, indicating that afforestation could have a significant effect on ecosystem CO_2 emissions. Even though photosynthesis of the understory vegetation in both alfalfa and Walker plots had a confounding effect on soil respiration in 2007, the average soil respiration rate during the growing season in the alfalfa plots still tended to be greater than that in the Walker plots. We expect that the difference between the two land use systems would have been much greater in 2007 had the soil respiration rate measurement not been confounded by the photosynthesis of weeds and the crop, because the rate of photosynthesis (and thus the uptake of CO_2) would have been much greater in the alfalfa than in the Walker plots, since plant biomass per unit area was much greater in the former than in the latter (personal observation).

The current results compare well with Paul et al. (1999) who found that field CO_2 production in an alfalfa field was higher than that in a hybrid poplar plantation (planted in 1989) in both 1993 and 1994, but was inconsistent with the land use effect data in the first year after land use conversion (Saurette et al. 2008), where no land use effect on soil respiration rates was found when barley was converted to Walker poplar. The land use effect on soil respiration could have been caused by changes in soil temperature and soil water content (Qi and Xu 2001, Rodeghiero and Cescatti 2005, Gaumont-Guay et al. 2006). However, that was not the case in our study, as soil temperature in the Walker plots was even higher than that in the alfalfa plots and no land use effect was found on soil water content. Soil organic carbon and nitrogen content and other possible factors affecting soil respiration (Rodeghiero and Cescatti 2005, Kirschbaum 2006) were also not different between the two land uses (Saurette et al. 2008a). Since seasonal trends of soil respiration were always similar between the two land uses, and the management practices were also similar (between the different crops, i.e., barley and alfalfa) among the different years, I suggest that the difference in the land use effects between the years was a result of the different crop species used in the rotation.

Plant species could affect soil respiration (Paul et al. 2002). Alfalfa is one of the most important forage crops widely grown in the region, and it has the ability to fix nitrogen, which is a very energy consuming biological process (Hopkins, 1999). During the biological nitrogen fixation process, N-fixing bacteria oxidize organic carbon to produce energy, releasing large amounts of CO_2 in the process. However, in Saurette et al. (2008a) the crop plots were planted to barley which does not biologically fix nitrogen, and thus has a much lower CO_2 emission density than the alfalfa. Soil respiration could also be affected by different quantities and quality of fresh carbon input (Li et al. 2005). Large quantities of the alfalfa residue with low C:N ratios were mixed into the soil during cultivation and that became a large source of CO_2 when the alfalfa residue decomposed. The quantity of litter input to the soil in the Walker poplar plots was much smaller and the litter would also have greater C:N ratios. Residue with a high C:N ratio is difficult to decompose and would release C slowly.

The alfalfa ecosystem accumulated carbon, while the plantation ecosystem lost carbon in 2008 in the fourth growing season after land use conversion (Fig. 9). The Walker poplar plantation was postulated to be a carbon sink due to its low heterotrophic respiration. However, considering the low survival rate (29%) resulted from frost damage in the cold winters and by browsing, the carbon loss in the plantation may not be unexpected. Furthermore, even though the alfalfa ecosystem sequestered carbon, the heterotrophic respiration was much greater than that in the Walker plantation, which implied that the soil in the alfalfa plots lost much more carbon and was more sensitive than the Walker poplar plots.

4.2. Land use effects on the temperature sensitivity of soil respiration

The long-term Q_{s10} not only represents a temperature effect on soil respiration, but also includes the effects of some other abiotic factors (e.g., soil water content) and biotic factors (e.g., microbial activities and root dynamics) on soil respiration (Davidson et al. 2006). The R_{s10} and Q_{s10} values in our study are well within the range of 0.7 – 4.9 for R_{s10} and 2.0 – 6.3 for Q_{s10} reported by Davidson et al. (1998) and Jansen et al. (2003) for European and North-American forest ecosystems. The Q_{s10} values in the Walker plots in both years were similar to that reported by Gaumont-Guay et al. (2006) in a boreal aspen stand ($Q_{s10} = 3.8$) and Wang et al. (2006a) in an aspen-birch forest ($Q_{s10} = 3.75$) in northeastern China.

The higher long-term Q_{s10} values in the alfalfa than in the Walker plots in both years were most interesting. This result implies that an increase in temperature would cause a greater impact on the rate of soil respiration in the alfalfa than in the Walker poplar plots. Many factors could affect temperature sensitivity of soil respiration, such as soil water content, substrate quality, and microbial population (Davidson et al. 2006). Furthermore, temperature sensitivity of root respiration could contribute more to that of soil respiration than could that of heterotrophic respiration (Boone et al. 1998). In the current study, the higher temperature sensitivity in the alfalfa plots could be due to the unique alfalfa and hybrid poplar root systems and the associated exudation of soluble organic C and microbial populations. The composition of microbial populations can change quickly as prevailing soil conditions at a locality select for microbial communities with particular adaptations to temperature and biotic control have an impact on the types and rates of carbon mineralization (Balser and Wixon 2009). In addition, more frequent activity, cultivation for example, of land uses might also cause higher temperature sensitivity of soil respiration (Sheng et al. 2010).

Short-term Q_{s10} represents the instantaneous response of certain respiring biological entities to short-term soil temperature changes (Davidson et al. 2006). In contrast to the land use effect on the long term Q_{s10}, the short term Q_{s10} in the Walker plots was greater than that in the alfalfa plots. These contrasting results could derive from the different representation of short- and long-term Q_{s10}. As pointed out by Davidson et al. (2006), the long-term Q_{s10} partly represents the response of soil respiration to the phenological events, i.e., fine root growth, litter fall. In the short term, the soil respiration in the Walker plots might change more with soil temperature than in the alfalfa plots, while the soil respiration changed much more with the phenological events of alfalfa plots than the Walker plots. Furthermore, the short-term Q_{s10} value was higher in the colder months in both land uses in 2008, consistent with Davidson et al. (1998) and Janssens and Pilegaard (2003). Increasing temperature in cold environment could activate dormant microbes and rapid change in microbes might result in the larger Q_{s10} (Janssens and Pilegaard 2003). Considering that the Q_{s10} value varies from month to month and the Q_{s10} function accurately estimates annual soil respiration (Davidson et al. 1998), when annual soil respiration is estimated it is better to use the short-term Q_{s10} (Janssens and Pilegaard 2003).

4.3. Temporal variations of soil respiration

While a comparison on the inter-annual variation in soil respiration is not possible in this study because of the different methods used for soil respiration measurement in the two years, our study indicated that soil respiration can have large seasonal and diurnal variation (Fang et al. 1998, Xu and Qi 2001a, Gaumont-Guay et al. 2006, Wang et al.

2006a). In this study, soil temperature accounted for most of the seasonal variation in soil respiration, including both night-time average and daily average respiration in 2008. The small peaks of soil respiration occurring at the end of the growing season in both land uses and years were likely induced by the sudden increase in soil temperature (Fig. 1) and/or decomposition of litter and alfalfa residue. Temperature affects the respiratory enzymatic activity, the affinity of the enzyme for substrates and the substrate availability to respiratory enzymes indirectly (Davidson et al. 2006). However, soil temperature only explained a small percentage of the temporal variation in soil respiration in 2007. The photosynthesis and respiration of understory vegetation in the chambers might have confounded the temperature effect on soil respiration, resulting in much less variance being explained by soil temperature.

Hysteresis was found between soil respiration and soil temperature in terms of the diurnal changes, consistent with Gaumont-Guay et al. (2006) and Tang et al. (2005). Gaumont-Guay et al. (2006) found that the peak of soil respiration was 3-5 hours later than that of soil temperature at 2 cm depth. Tang et al. (2005) also observed that hourly soil respiration decoupled with soil temperature at 8 cm depth. They all suggested that diurnal variation of rhizospheric respiration caused the hysteresis. As a component of soil respiration, rhizospheric respiration could be more controlled by photosynthates transported from leaves to roots than soil temperature, and time is needed for photosynthate transportation driven by diurnal buildup of photosynthates. In addition, abrupt decreases in soil respiration were observed in the early morning in both land uses and years. One potential reason was that the carbon sink competition among different tree components was switched (Gaumont-Guay et al. 2008b). For example, when the carbon supply is scarce, the shoot has a higher priority for the carbon supply than roots (Minchin and Lacointe 2005), as is in the case when plants prepare to resume photosynthesis in the morning. In contrast, some other studies found that diurnal variation of soil respiration was in phase with soil temperature (Drewitt et al. 2002, Shi et al. 2006). Those contradictory results might have been related to the size of heterotrophic respiration, which is tightly controlled by soil temperature; it's possible that heterotrophic respiration constituted the majority of soil respiration in Drewitt et al. (2002) and Shi et al. (2006). In addition, soil temperature at different depths was probably used and that might had caused the contradictory results.

5. Conclusions

Land use change had a significant effect on soil respiration in 2008 when the understory vegetation was controlled and their photosynthetic activities in the chambers were eliminated by keeping the soil respiration measurement chamber dark. However, when the photosynthetic activities of the understory vegetation confounded the soil respiration measurements in 2007, no land use effect on soil respiration was observed. With the greater long-term R_{s10} and Q_{s10} in the alfalfa plots, soil respiration in the alfalfa plots was more sensitive to temperature changes than that in the Walker plots under future warmer climatic scenarios. The NEP of the alfalfa ecosystem was greater than that of the Walker poplar plantation in year three and four after the implementation of the afforestation treatment because of the slow establishment of the hybrid poplar plantation.

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Table 2 - 1. Short-term soil respiration at 10 °C ($R_{s10n'}$) and temperature sensitivity of soil respiration ($Q_{s10n'}$) for each month calculated based on daily mean night-time soil respiration and daily mean night-time soil temperature at 5 cm. Values in the Table are means ± standard errors.

Month	R_{s10} (μmol m^{-2} s^{-1})				Q_{s10}			
	2007		2008		2007		2008	
	Alfalfa	Walker	Alfalfa	Walker	Alfalfa	Walker	Alfalfa	Walker
June	/*	/	3.6±0.3	2.4±0.1	/	/	2.6±0.2	4.2±0.6
July	2.1±1.1	2.4±0.02	5.2±0.9	3.1±0.1	4.3±1.8	1.6±0.1	2.1±0.1	2.0±0.02
August	2.4±0.3	1.9±0.1	5.6±0.6	3.2±0.2	3.5±1.0	1.9±0.2	1.6±0.1	3.2±0.9
September	2.7±0.3	1.9±0.2	4.4±0.8	4.0±0.1	3.3±0.6	2.5±0.6	3.4±1.2	3.7±1.4
October	/	/	3.5±0.2	2.6±0.1	/	/	3.2±0.2	4.0±0.6
Mean	2.4±0.2	2.1±0.2	4.4±0.5	3.0±0.4	3.7±0.3	2.0±0.2	2.6±0.4	3.4±0.5

*: In June, no significant exponential relationship was found; in October, not measured.

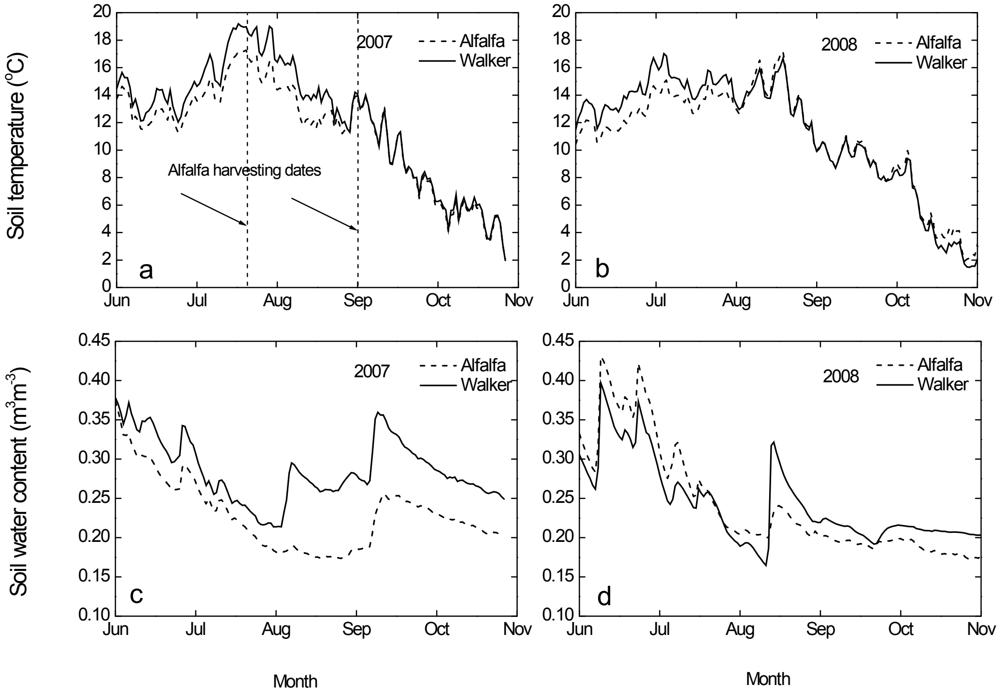

Figure 2 - 1. Daily mean soil temperature at 10 cm depth from June to November in (a) 2007 and (b) 2008 for both alfalfa (dashed) and Walker (solid) plots and soil water content at 10 cm depth from June to November in (c) 2007 and (d) 2008 for both land uses.

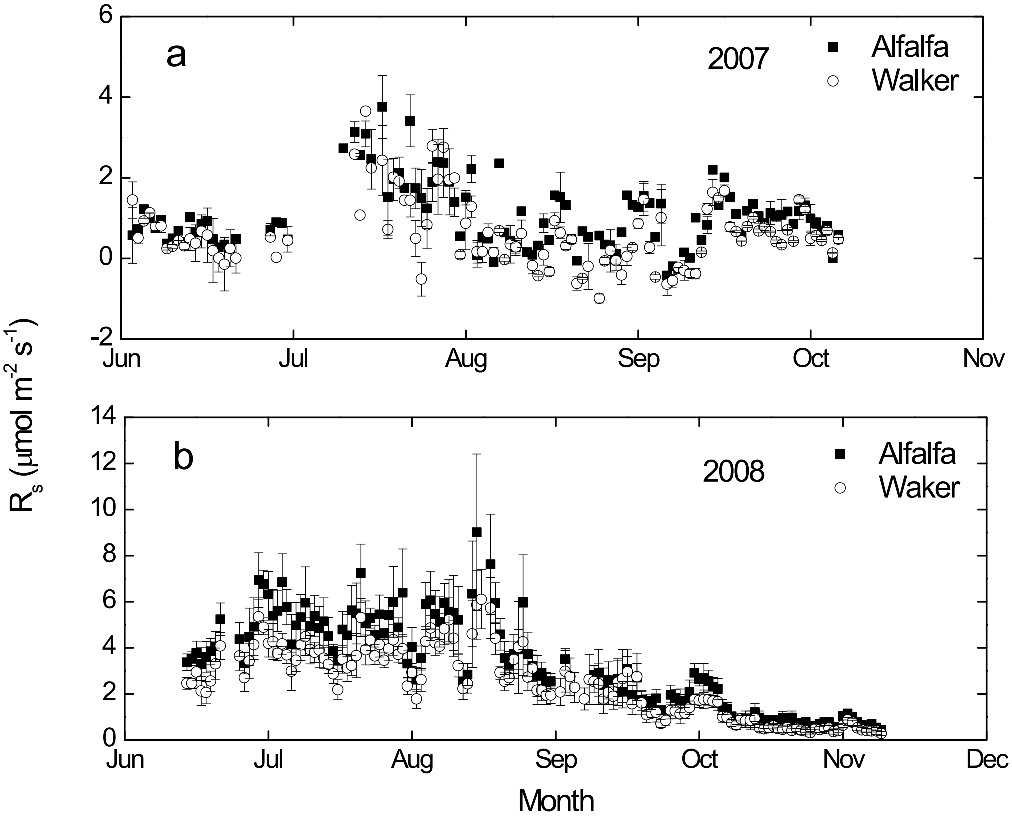

Figure 2 - 2. Daily mean soil respiration (R_s) (a) from June to October in 2007 and (b) from June to November in 2008. Note that the soil respiration measured in 2007 had the contribution of understory vegetation in the chamber, but not in 2008 (the same below).

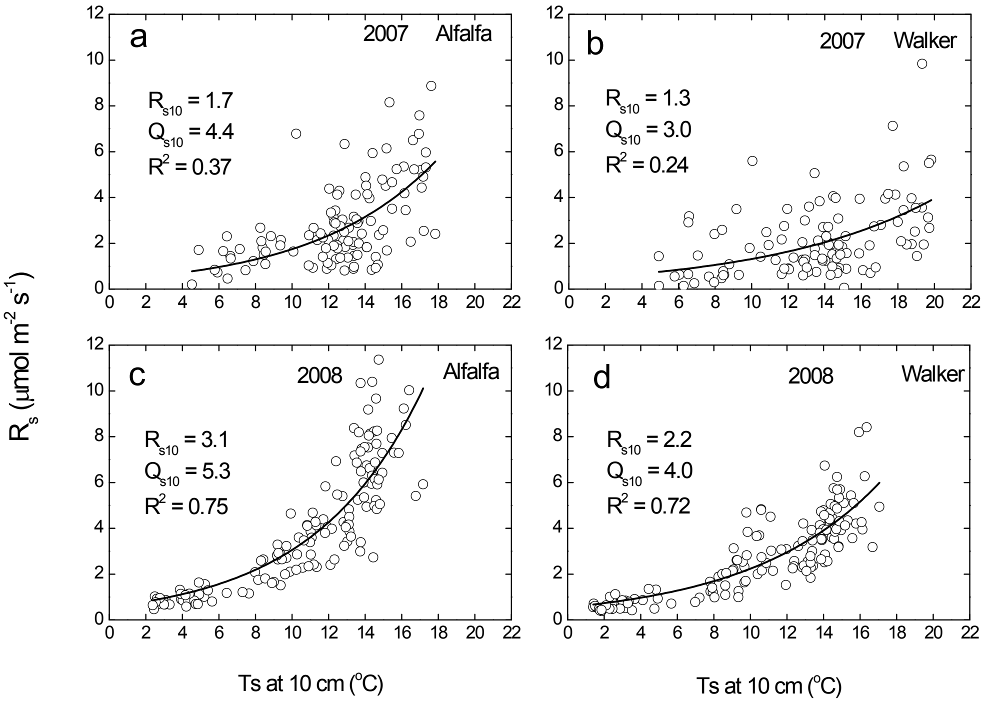

Figure 2 - 3. Relationships between daily mean night-time soil respiration (R_{sn}) and daily mean nighttime soil temperature (T_{sn}) at 10 cm depth in both land uses in 2007 and 2008.

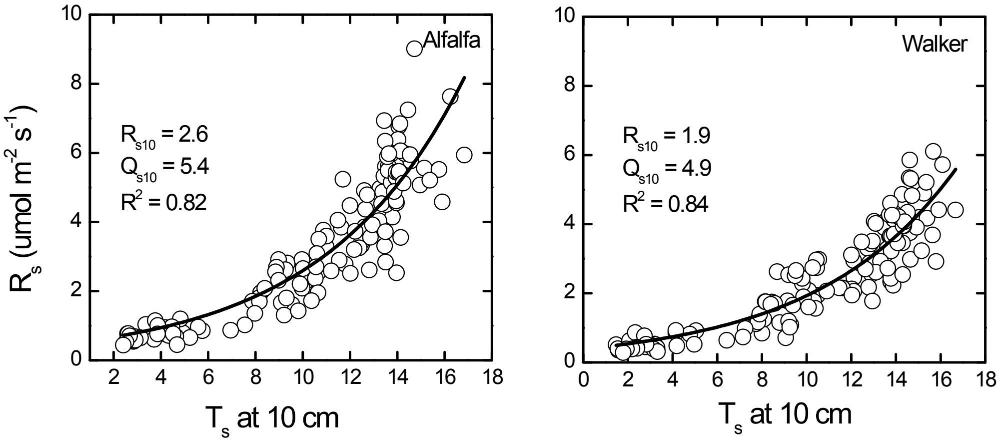

Figure 2 - 4. Relationships between daily mean soil respiration (R_s) and daily mean soil temperature (T_s) at 10 cm depth in both land uses in 2008.

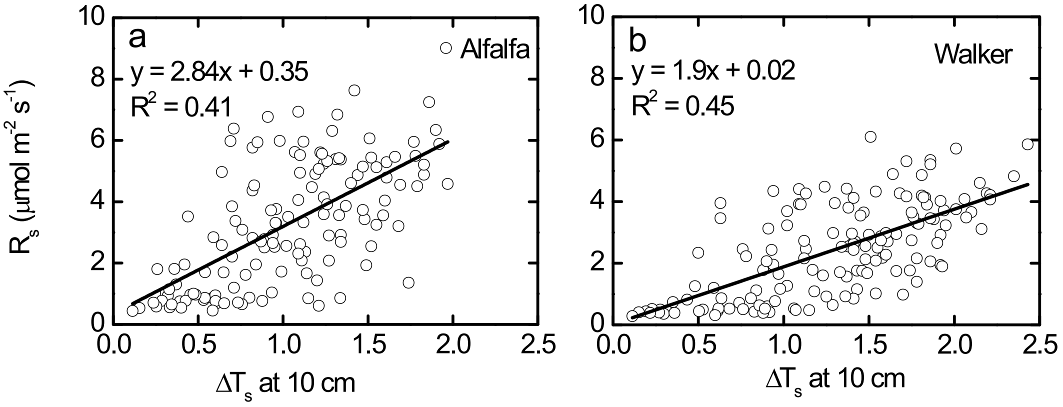

Figure 2 - 5. Relationships between daily mean soil respiration (R_s) and range of daily soil temperature (ΔT_s) at 10 cm depth in both land uses in 2008.

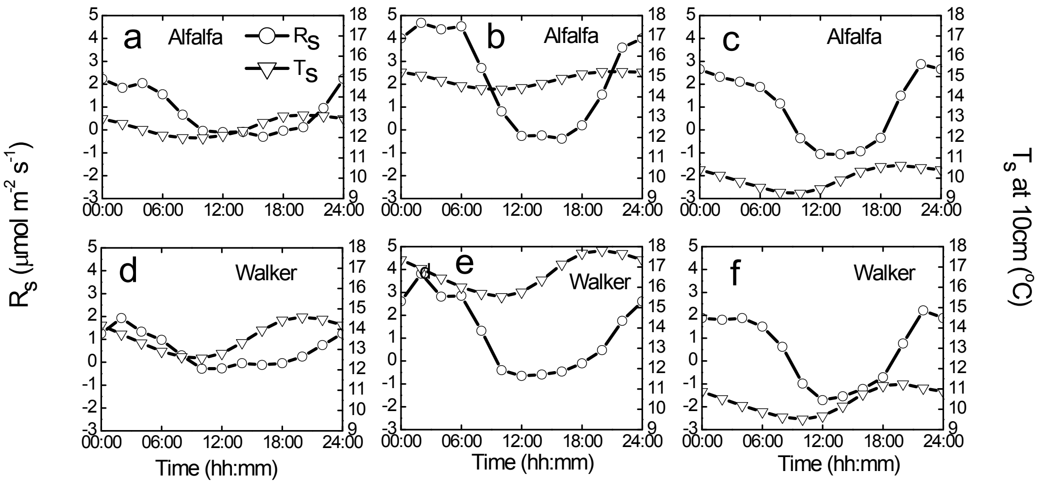

Figure 2 - 6. Diurnal variation of bihourly mean soil respiration (R_s) and bihourly mean soil temperature (T_s) at 10 cm depth during the early [(a) and (d), 1-30 June], mid [(b) and (e), 1-30 July)] and late [(c) and (f), 15 August to 15 September)] growing seasons of 2007 in both land uses.

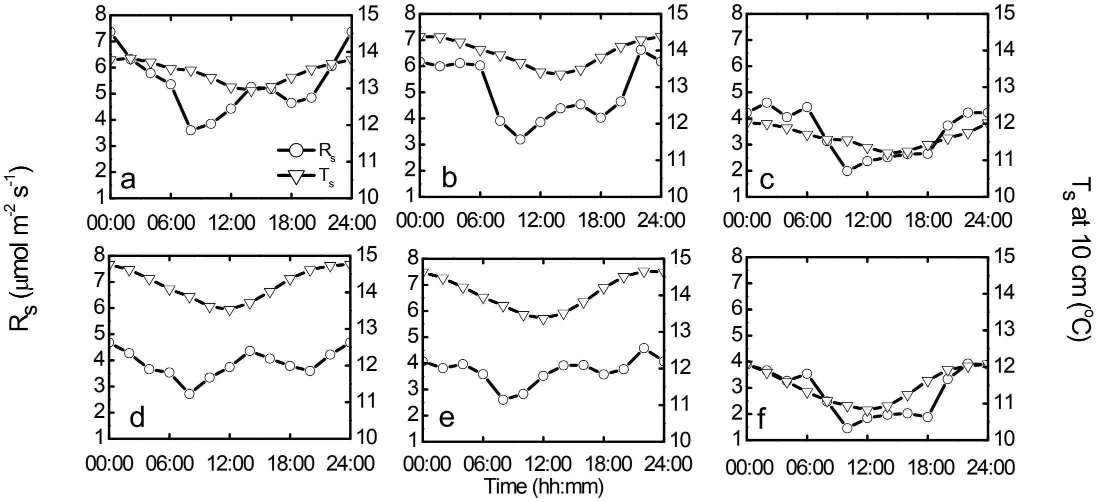

Figure 2 - 7. Diurnal variation of bihourly mean soil respiration (R_s) and bihourly mean soil temperature (T_s) at 10 cm depth during the early [(a) and (d), 1-30 June], mid [(b) and (e), 1-30 July] and late [(c) and (f), 15 August to 15 September] growing season of 2008 in both land uses.

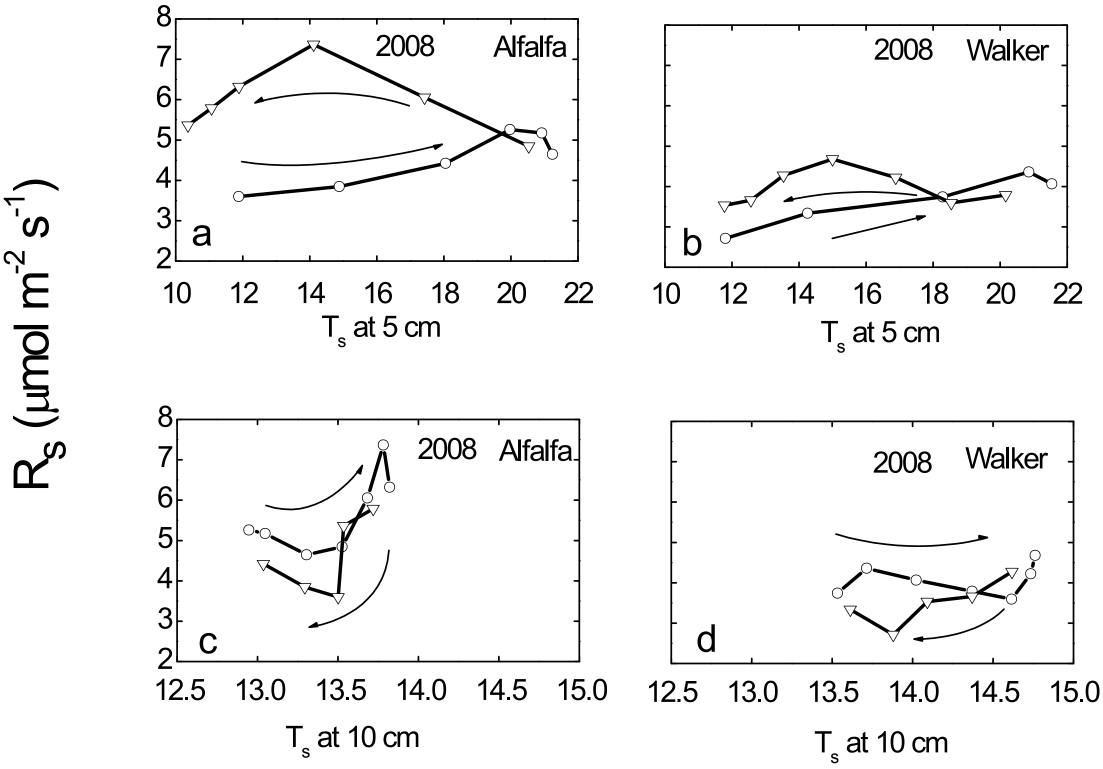

Figure 2 - 8. Relationships between bihourly mean soil respiration (R_s) and bihourly mean soil temperature (T_s) at 5 [(a) and (b)] or 10 cm depth [(c) and (d)] in June, 2008.

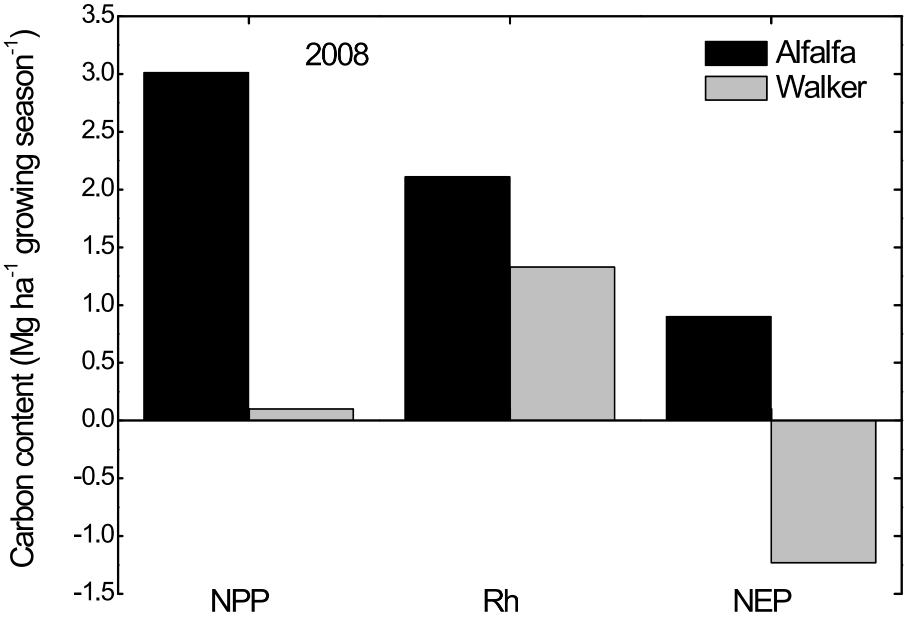

Figure 2 - 9. Net primary productivity (NPP), heterotrophic respiration (R_h) and net ecosystem productivity (NEP) over the growing season (150 days) for both land uses in 2008. Note that tree survival rate was low (29%).

Chapter 3 Soil respiration and net ecosystem productivity in different aged hybrid poplar plantations in central Alberta

1. Introduction

Stand age can have a major effect on the net ecosystem productivity (*NEP*) of forest ecosystems (Litvak et al. 2003a, Kolari et al. 2004, Grant et al. 2007b, Noormets et al. 2007, Vargas et al. 2008, Black et al. 2009, Zha et al. 2009). Net ecosystem productivity is the balance between net primary productivity (*NPP*) and heterotrophic respiration (R_h) (Howard et al. 2004), both of which will change as stands develop. In the initial years after a forest plantation is established or natural forest ecosystem is recovered from some form of disturbance, heterotrophic respiration from the decomposition of residues and soil organic matter is typically greater than CO_2 uptake by photosynthesis (Grant et al. 2007a), and thus the plantations would act as a net carbon (C) source at that stage. After establishment, *NPP* increases rapidly due to rapidly increased leaf area index and greater photosynthetic capacity of the trees and R_h decreases because of the depletion of easily decomposable substrates and lack of major new labile C supply (Grant et al. 2007b). Now forest stands might turn into net C sinks. 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 become a C source again.

Much research has been done on how *NEP* changes with stand age in natural (Litvak et al. 2003a, Humphreys et al. 2006, Thuille and Schulze 2006, Noormets et al.

2007, Zha et al. 2009) or managed forests (Noormets et al. 2007, Yang et al. 2007, Black et al. 2009, Karu et al. 2009) after disturbances (e.g., logging, fire, or mining). For example, *Litvak et al.* (2003a) found that after fire, the C sink capacity of boreal black spruce (*Picea mariana*) stands in central Manitoba increased from 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*) stands turned into C sinks from sources with stand age until age 29 and then the C sink capacity declined with age, based on a chronosequence with 2-, 10-, 29-, and 90-year-old stands.

Soil respiration (R_s), which includes root or autotrophic respiration (R_a) and heterotrophic respiration (R_h), is a major contributor to the forest C balance (Ryan and Law 2005, Gaumont-Guay et al. 2009). Forest stand development has a significant influence on soil respiration (Wiseman and Seiler 2004, Saiz et al. 2006, Tedeschi et al. 2006, Ball et al. 2007). *Saurette et al.* (2006) found that soil respiration measured using static chambers increased with stand age in three different aged hybrid poplar (*Populus deltoides* x *Populus* x *petrowskyana* var. Walker) plantations (3-, 9- and 11-year-old) in the boreal forest ecological region. Similarly, *Arevalo et al.* (2010) observed that soil respiration in a 9-year-old Walker hybrid poplar plantation was greater than that in a 2-year-old hybrid poplar plantation in northern Alberta, within the same ecological region to that of our study site. In a boreal black spruce chronosequence, *Bond-Lamberty et al.* (2004a) reported that soil respiration generally increased with stand age from 4 to 21 years old, except for a 7-year-old stand which had the smallest respiration rates, and decreased from 21 to 152 years old. However, *Tedeschi et al.* (2006) found that soil respiration decreased with stand age in coppiced oak (*Quercus cerris* L.), in central Italy (Chronosequence: 1-, 5-, 10- and 17-year-old). A similar result where soil respiration decreased with stand age until 31 years old and then levelled out in the older stands (Chronosequence: 10, 15, 31, and 41 years old) was observed by *Saiz et al.* (2006) over a chronosequence of first rotation Sitka spruce (*Picea sitchensis*) plantations in central Ireland. However, *Tang et al.* (2009a) found that cumulative soil respiration increased with stand age, peaked at an intermediate age and then declined with stand age in a chronosequence of deciduous hardwood forests in Wisconsin and Michigan where cumulative soil respiration increased with stand age, peaked at intermediate age and then declined with stand age.

In Canada, ongoing afforestation programs on previously agricultural land, especially planting of short-rotation woody crops such as hybrid poplars, have been considered as an effective way to mitigate net CO_2 emissions (FAO 2004). Alberta-Pacific Forest Industries Inc. (Al-Pac) is an industrial leader in hybrid poplar plantation establishment in western Canada. They are currently planting about 1,200 hectares of hybrid poplar plantations each year and will eventually reach a total plantation estate of 25,000 hectares on 20- to 25-year rotations. Establishment of hybrid poplar plantations at such a scale will have significant implications not only for the wood supply for 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 soil respiration and net ecosystem productivity has been carried out on these plantations established on previously agricultural lands (Saurette et al. 2006, 2008b). *Saurette et al.* (2006) studied the stand age effect by measuring soil respiration on four selected sites using a static chamber system. Their manual and infrequent measurements could not sufficiently account for the soil respiration of the whole growing season. In addition, the temperature sensitivity of soil respiration could not be adequately tested when soil respiration measurements were limited to a few points in the growing season. The diurnal variations of soil respiration in the hybrid poplar plantations were also not thoroughly studied. In the current study, we used automated chamber systems to measure soil respiration every two hours to investigate (1) changes in soil respiration and its temperature sensitivity in the different aged hybrid poplar plantations, (2) the patterns of seasonal and diurnal variations of soil respiration in the plantations; one of the issues that particularly interested us was the question of temperature control on the seasonal dynamics and diurnal changes of soil respiration, and (3) the interannual variability of NEP and changes in NEP with stand age to examine the age at which (if ever) hybrid poplar stands shift from a net C source to a net C sink.

2 Methods

2.1 Site description

The study site is located near the Al-Pac mill (54°49´N, 113°31´W), in the southern area of the Boreal Mixedwood ecological subregion in northern Alberta, Canada. The climate in this area is continental, with warmer summers and long, cold winters. The growing season is about 175-180 days, from May to October (Government of Alberta, 2006). Climate normals from 1971-2000 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). Aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus* *balsamifera* L.), white spruce (*Picea glauca* Voss), and jack pine on upland terrain are the dominant native tree species in this area (Natural Regions Committee, 2006). Level to gently undulating plains are the primary landforms and the dominant soil type is Gray Luvisol, with Dystric and Eutric Brunisol occurring in the coarse textured soil areas (Natural Regions Committee, 2006).

Three different aged hybrid poplar (Walker) plantations were selected in 2007: Field 28S (F28S) planted in 2004, Field 28N (F28N) planted in 2001, and Field 1 (F1) planted in 1993. One more plantation, Field 8 (F8) planted in 1995 with the same clone, was added in 2008. However, due to logistical power supply problems to operate the equipment in F1, this site was abandoned in 2009. The crown closured status of the F1 site meant that little light penetrated through the canopy and the solar panels did not generate enough power to operate the automated soil respiration systems. All the selected plantations were established on previously marginal agricultural land and had high variability of soil organic C and nitrogen contents in appendix I (Saurette et al. 2006, Teklay and Chang 2008). Soil characteristics in these four different aged plantations can be found in *Saurette et al.* (2006) and *Teklay and Chang* (2008). All the stand ages in the current study were expressed as the age in 2009.

2.2 Root exclusion treatments to determine heterotrophic respiration rates

Two root-exclusion and two control plots (1 x 1 m) were established in each plantation in late May of 2009 to allow heterotrophic respiration rates to be quantified. The root-exclusion plots were set up by trenching soil to 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.

The trench was lined with a polypropylene landscaping fabric, which allowed water to go 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.

2.3 Soil respiration measurement

Soil respiration was measured using a non-steady state automated chamber system (ACS) from June to early October in 2007, June to early November in 2008, and June to early October in 2009. During the 2007 and 2008 measurements, each ACS was equipped with three chambers (52.5 cm internal diameter, 50 L volume) with dome-shaped lids. In 2009, each ACS was equipped with four chambers, two placed in the control plots and the other two in the root exclusion plots, within each stand age of the chronosequence. The chambers were closed sequentially for one minute every two hours for measuring the rate of soil respiration using an infrared gas analyzer (IRGA, LI810 CO_2/H_2O analyzer). At each measurement cycle, the CO_2 concentration within the chamber was determined every second for one minute. The slope of the CO_2 concentration increase was derived using linear regression and the rate of soil respiration was calculated using the following equation:

$$\mathbf{R_s} = \rho_a \frac{V}{A} \frac{ds_c}{dt}$$

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 lids were kept open when the chambers were not in use to allow rain and litter to fall into the collar area.

In 2007, understory vegetation was allowed to grow in the chambers. Soil respiration measured in the daytime was CO_2 efflux from soil reduced by photosynthetic uptake of CO_2 by the understory vegetation in the chambers. In 2008 and 2009, 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. Therefore, the confounding effect of photosynthetic CO_2 uptake was removed from explaining the variation of soil temperature on soil respiration.

Mean heterotrophic respiration (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.* (2008b) for four different aged hybrid poplar plantations in the same area as our study. In order to remove soil respiration caused by decomposition of severed roots in the trenched plots in 2009, a correction factor of 0.83, determined by *Saurette et al.* (2008b), was used. Mean heterotrophic respiration throughout the growing season in 2009 was calculated using mean soil respiration in the root exclusion plots multiplied by the correction factor.

2.4 Net primary productivity (NPP) and Net ecosystem productivity (NEP)

A 15 x 15 m plot was established in each plantation for tree measurement. Diameter at breast height (DBH) and total height (H) were measured for each tree in the plot at the beginning of the first growing season of this study (2007) and then at the end of each growing of this study. The aboveground biomass without leaves was determined using the biomass equations established by *Saurette et al.* (unpublished):

$$Aboveground\ \ Biomass(kg) = 0.6298 * DBH^{1.3582} * H^{0.2353}$$

Root biomass for the two younger plantations was calculated using the equation established by *Saurette et al.* (unpublished):

$$Belowground\ \ Biomass(kg) = 1.1810 * DBH^{2.5123} * H^{-2.1616}$$

Root biomass for the two older plantations was calculated as follows (Fang et al. 2007):

Oven-dry root biomass (RB, kg) = EXP (3.97-252.92 / (DBH x H))

Thirteen round litter traps with an internal diameter of 30 cm were randomly distributed in each plot to collect litterfall (LF). The collected LF was oven-dried at 65 °C until constant weight and weighed in the laboratory. The C content of aboveground, root and litterfall was calculated by multiplying a standard factor of 0.5 (Pregitzer and Euskirchen 2004). The *NPP* equals the difference in biomass C between the beginning and the end of the growing season plus litterfall:

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

The NEP is then determined using the following equation:

$NEP = NPP - R_h$.

2.5 Soil temperature and soil water content measurement

Soil temperature was measured every two hours at 5 cm depth with a copper-constantan thermocouple (Omega Engineering, Montreal, QC) placed near the chambers. Soil temperature at 10, 20, 30 and 40 cm depths was measured every hour with the same type of thermocouples and the data was logged with Campbell Scientific CR10X dataloggers (Campbell Scientific Inc., Logan, UT). Volumetric water content at 10 and 20 cm depths was measured every hour using Campbell Scientific CS616 water content reflectometers (Campbell Scientific Inc., Logan, UT) and datalogged with CR10X datalogger.

2.6 Data analysis

The relationship between daily mean R_s and T_s at 10 cm was analyzed by the following Q_{10} model:

$$\mathbf{R_s} = R_{s10}\, Q_{S10}^{(Ts-10)/10}$$

where R_s is the soil respiration rate (µmol m^{-2} s^{-1}), R_{s10} is soil respiration rate at 10 °C, Q_{s10} is temperature sensitivity of soil respiration, which is defined as the relative increase in soil respiration for a 10 °C increase in soil temperature, and T_s is soil temperature (°C).

The difference in soil respiration among the different aged plantations over the measurement period was tested using repeated measures ANOVA at a significant level of

$\alpha = 0.05$ in SAS 9.0 (Version 9.0, SAS institute Inc.), considering day as repeated measures. The normality of distribution and homogeneity of variance were also tested using SAS 9.0. Linear or nonlinear curve fitting was done in Origin (Version 8.0, OriginLab Corp.).

The statistical model for repeated measures ANOVA was:

$$Y_{ijk} = \mu + T_i + D_j + TD_{ij} + \varepsilon_{ijk}$$

Where:

Y_{ijk} = a dependant variable (soil respiration)

μ = overall mean

T_i = the *i*th treatment (different aged plantations) (fixed factor)

D_j = the jth day (fixed factor)

T_iD_j = the interaction of treatment * day

ε_{ijk} = random error associated with the day * treatment

3 Results

3.1 Soil temperature and soil water content

Soil temperature (T_s) at 10 cm depth followed similar seasonal trends in the different aged hybrid poplar plantations throughout the growing season from 2007 to 2009 (Fig. 3-1) and showed a similar trend at the other depths (data not shown) to that at 10 cm for each plantation. However, seasonal trends of T_s were different among the three years with different peak times in each of the growing seasons (Fig. 3-1a, 3-1b and 3-1c). Soil temperature was consistently lower in older than in younger plantations until soil temperature peaked, and then became warmer in older than in younger stands thereafter.

Soil water content at 10 cm depth was higher in the two younger (5- and 8–year-old in 2009, same below) than in the older plantations (14- and 16-year-old) during the growing seasons, with similar seasonal trends among the plantations (Fig. 3-1d, 3-1e and 3-1f). Soil water content was all within optimum conditions for microbial and tree growth during measurement periods. Soil water content at 20 cm depth (data not shown) had a similar trend to that at 10 cm depth for each plantation. The substantial drawdown of soil water content by evaporation of the trees in the two older stands was evident (Fig. 3-1).

3.2 Seasonal variation of soil respiration

Similar seasonal variations of R_s among the different aged plantations were observed in each year (Fig. 3-2). However, the patterns of seasonal variation in 2007 and 2008 (Fig. 3-2a and 3-2b) were different from that in 2009 (Fig. 3-2c), with different peak times in the growing seasons.

In July and August of 2007, R_s was different between the 5- and 8-year-old plantations, and between the 5- and 16-year-old plantations (no data were recorded in September in the 8-year-old plantation), but not between the 8- and 16-year-old plantations (Fig. 3-2a). In 2008, R_s in the 14-year-old plantation was significantly higher than that in the other three plantations in June and July (no data available in June in the 16-year-old plantation), but not in August, September or October (Fig. 3-2b). No difference in R_s was found among the 5-, 8- and 16-year-old plantations in the 2008 measurement period (Fig. 3-2b). In 2009, R_s in the 14-year-old plantation was higher than that in the 5- and 8-year-old plantations, except that in June no difference was observed between the 14- and 5-year-old plantations. The R_s was also different between the 5- and 8-year-old plantations in June, but not in the other months (Fig. 3-2c).

An exponential relationship between daily mean R_s and T_s at 10 cm was found in all the studied plantations (Fig. 3-3). The T_s at 10 cm explained much less of the variation of R_s in 2007 and 2009 than in 2008 (Fig. 3-3a and 3-3c). In 2007 and 2009, more of the variation in R_s was accounted for 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 8- and 14-year-old plantations in 2008 and in the 14-year-old in 2009 among the plantations. The Q_{s10} value in the 5-year-old plantation in 2007 was out of the biologically valid range of Q_{s10}.

Negative and positive linear relationships between R_s and soil water content were found in the 5-year-old plantation in 2007 and 2008, respectively (Fig. 3-4a and 3-4c). A quadratic polynomial relationship between R_s and soil water content was also found in the 14-year-old plantation in 2008 and 2009, and in the 16-year-old plantation in 2007 (Fig. 3-4b, 3-4d and 3-4e).

3.3 Soil respiration in the trenched plots in 2009

Soil respiration in the trenched plots, referred to as heterotrophic respiration (R_h), had similar seasonal trends to R_s in all three plantations (Fig. 3-5 and 3-2c). Respiration rates 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. 3-5). The R_h accounted for 66, 70, and 66% (after multiply the correction factor, 0.83) 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. 3-6).

Soil temperature at the 10 cm depth had an exponential relationship with R_s in both the control and root exclusion treatments (Fig. 3-7). The Q_{s10} values in the root exclusion treatment were greater than those in the control in the 14-year-old plantations, while in the 5- and 8-year-old plantation Q_{s10} was lower in the root exclusion treatment than in the control. The R_{s10} was always higher in the control than in the root exclusion plots.

3.4 Diurnal variation of soil respiration

Diurnal variation of bihourly measured R_s had similar trends among the three plantations in 2007, with a mid-day minimum (around 12 h) and late evening maximum (around 0 h) (Fig. 3-8a, 3-8b and 3-8c), lagging T_s at 10 cm by 2 to 4 hours. 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. 3-8d and 3-8e) or late evening (around 22 h) in the two older plantations (Fig. 3-8f and 3-8g). 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-year-old plantation. In the two older plantations, 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 the three plantations (Fig. 3-8h, 3-8i and 3-8j). In contrast, root R_s (or autotrophic respiration) increased from 18 h, peaked in late night (around 2 h) and levelled out in the daytime in the youngest plantation (Fig. 3-8h). No evident diurnal variation of root R_s was observed in the two older plantations (Fig. 3-8i and 3-8j).

3.5 Net ecosystem productivity

Net primary productivity (*NPP*) increased with plantation age in 2008 and 2009, with the 14-year-old plantation had the greatest amount of litterfall in both years (Fig. 3-9). The 14-year-old plantation always had the largest R_h among the studied plantations in both years. Net ecosystem productivity (*NEP*) increased with plantation age in both years, with negative values in the youngest plantation (F28S) in 2008 and in the two younger plantations in 2009, and positive values in the older plantations in both years.

4. Discussion

4.1 Soil respiration in the different aged plantations

The oldest plantation (16-year-old in 2009) will be treated differently in the discussion of soil respiration considering its markedly different soil properties, e.g., soil organic matter content, soil texture (Saurette et al. 2006), that could significantly confound the age effect. In general, soil respiration in the 16-year-old plantation was lower than that in the 14-year-old in 2008, even though the fine root biomass (reflecting the greatest standing biomass in that stand) and dissolved organic C content in the oldest stand was greater than that in 14-year-old stand (Saurette et al. 2008b, Teklay and Chang 2008). The lower soil organic matter and soil water contents and coarser soil texture could mute the effect of fine root biomass and dissolved organic C on soil respiration and result in lower soil respiration in the 16-year-old stand.

In general, the increasing soil respiration with stand age in 2007, 2008 and 2009 was consistent with that reported by *Saurette et al.* (2006) in the same study sites. This was also consistent with studies on hybrid poplars at another site in central Alberta by *Arevalo et al.* (2010), in a boreal black spruce chronosequence in Manitoba by *Bond-Lamberty et al.* (2004a), in a loblolly pine (*Pinus taeda*) chronosequence ranging from 1 to 25 years old by *Wiseman and John* (2004). *Tang et al.* (2009a) reported that soil respiration increased from stand establishment until an intermediate age in a chronosequence of deciduous forests in Wisconsin and Michigan. In contrast, no significant difference was found in another four different aged hybrid poplar plantations (Saurette et al. 2008b), which was potentially affected by the low number of replications (two replicates) used that lowered the power of test. In a Sitka spruce chronosequence (ranging from 10 to 47 years old) in central Italy, *Saiz et al.* (2006) found that soil respiration decreased with stand age. Those examples illustrate that soil respiration rates may not follow a set trajectory with stand development.

The difference in soil respiration with stand age could be caused by many factors, such as differences in root biomass, soil organic C and dissolved organic C contents, and the amount of litterfall as a potential source of labile organic C input. Root biomass tends to increase with stand maturation and can cause the stand age effect on soil respiration (Wiseman and Seiler 2004). *Saurette et al.* (2008b) reported that fine root biomass 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 soil respiration through input of labile organic C (Yan et al. 2006).

4.2 Seasonal variation and temperature sensitivity of soil respiration

Similar to what have been reported by several others (Rayment and Jarvis 2000, Gaumont-Guay et al. 2006, Tang et al. 2009a), seasonal variation in soil respiration was observed in the different aged plantations in all three years in this study. In general, seasonal variation of soil respiration was driven by soil temperature, possibly modified by soil water content (Fig. 3 and 4), as further discussed below. In 2008, soil temperature explained most of the seasonal variation in soil respiration, while soil water content, which has been found to significantly influence soil respiration in some research (Davidson et al. 1998, Jassal et al. 2008), was not a limiting factor (mostly above 0.2 m^3 m^{-3}) in our 2008 study. However, soil temperature only explained a small part of the variation in soil respiration in 2007 and 2009. The photosynthesis and respiration of understory vegetation in the chambers in 2007 might have introduced significant variation in soil respiration, resulting in much less variation explained by soil temperature. In 2009, soil temperature varied between 13 and 18 °C from June to late September and might not have been a limiting factor and thus the lack of temperature control on soil respiration.

Temperature sensitivity of soil respiration as measured by Q_{s10} was different among the plantations. The greater Q_{s10} in the 8- and 14-year-old stands in 2008 and in the 14-year-old plantation in 2009 suggested that different dominant components (root and heterotrophic respiration) were probably involved in the various plantations. *Tedeschi et al.* (2006) found that temperature sensitivity of soil respiration decreased with stand age in a Mediterranean oak forest (ranging from 1 to 17 years old). The Q_{s10} value in the current study (excluding the 7-year-old stand) was 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 (*Populous davidiana* Dode and *Betula platyphylla* Suk.) forest (3.75) in northeastern China (Wang et al. 2006b). The greatest Q_{s10} value in the 8- and 14-year-old stand in 2008 and in the 14-year-old plantation in 2009 suggests that these two stands had the greatest sensitivity to temperature changes and might be more sensitive to the future climate warming scenarios in terms of CO_2 emissions. Q_{10} has been found to vary with both time and space (Xu and Qi 2001b, Janssens et al. 2003). When soil respiration is simulated using the Q_{10} model, selection of Q_{10} value should be depending on the objective of the model. If the model output is short-term respiration, the short-term Q_{10} should be used, avoiding over- or under-estimation (Xu and Qi 2001b). If the model is used to predict soil respiration in a large landscape area, spatially varied Q_{10} values are required for accurate simulation modeling. Therefore, considering the variations in temperature sensitivity of soil respiration with stand age, empirical models should take stand age effect into account when temperature sensitivity is used to predict soil CO_2 efflux.

Hysteresis was found between soil respiration and soil temperature in the diurnal measurements, consistent with *Gaumont-Guay et al.* (2006) and *Tang et al.* (2005). *Gaumont-Guay et al.* (2006) found that the peak of soil respiration was 3-5 hours later than that of soil temperature at 2 cm depth. *Tang et al.* (2005) also observed that hourly soil respiration decoupled with soil temperature 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. Moreover, the hysteresis could also be caused by the use of soil temperature determined at different soil depths. When great heterotrophic respiration occurred in deeper soil, the selection of soil temperature at shallower depth could result in the respiration-temperature hysteresis. In addition, abrupt decreases in soil respiration were observed in the early morning in the different aged plantations. One potential reason was that the C sink competition among different tree components was switched *Gaumont-Guay et al.* (2008b). For example, when the C supply is scarce, the shoot has a higher priority for the C supply than roots (Minchin and Lacointe 2005), as is in the case when plants prepare to resume photosynthesis in the morning. In contrast, some other studies found that diurnal variation of soil respiration was in phase with soil temperature (Drewitt et al. 2002, Shi et al. 2006). Those contradictory results might have been related to the size of heterotrophic respiration, which is tightly controlled by soil temperature; it's possible that heterotrophic respiration constituted the majority of soil respiration in *Drewitt et al.* (2002) and *Shi et al.* (2006).

4.3 Soil respiration in the trenched plot

The lack of stand age effect on the R_h: R_s ratio was found in the studied plantations, consistent with what *Saurette et al.* (2008b) reported (average R_h: R_s = 0.63) in another study involving four hybrid poplar plantations with different ages in the same study area. However, *Bond-Lamberty et al.* (2004a) 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 Mediterranean oak forest chronosequence. The R_h: R_s ratio in this study was much higher than those reported by others for boreal forests (Russell and Voroney 1998, Bond-Lamberty et al. 2004a). However, an even larger R_h: R_s ratio (0.78) was found by *Tedeschi et al.* (2006) in Mediterranean oak forests. This large R_h: R_s ratio could be an artefact. First, the decomposition of severed roots within the trenched plots may contribute to heterotrophic respiration (Gaumont-Guay et al. 2008a). Secondly, the roots of the understory vegetation could also have contributed a large portion of the heterotrophic respiration (Bond-Lamberty et al. 2004a), even though the aboveground understory vegetation was removed regularly. 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 the plantations. No dramatic shift between heterotrophic and root respiration was observed and root respiration was always low in the growing season (data not shown). This was in contrast with *Gaumont-Guay et al.* (2008a) who found that root respiration dominated soil respiration from mid-July to mid-September in their studied boreal black spruce stand. The greatest soil respiration in the trenched plot in the 14-year-old plantation could be attributed to the greater soil organic C content, the greater amount of litterfall (Fig. 9) and a large pool of dissolved organic C that can be easily decomposed (Teklay and Chang 2008).

4.4 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 C source and the two older plantations as C sinks. This result was similar to that of *Litvak et al.* (2003a) and *Zha et al.* (2009). *Zha et al.* (2009) observed that jack pine stands turned into a C sink from a C source as stands age and proposed that the change was due to the increased leaf area index along the chronosequence. *Litvak et al.* (2003a) also found a C source-sink shift with stand age in five different aged black spruce stands (ranging from 11 to 130 years old). The changes in NPP and NEP along the chronosequence in this study were consistent in both 2008 and 2009, suggesting that the stand age effect on NEP was determined by NPP.

Assuming a linear relationship between stand age and NEP, we can derive that C neutrality or the C balance (sink vs. source) compensation point of the plantations would occur between 7 (based on data in 2008) and 13 years old (based on data in 2009). This result was similar to that of *Litvak et al.* (2003a) and *Howard et al.* (2004). They found that black spruce and jack pine stands became C sinks from C sources at about 10 years old. *Humphreys et al.* (2006) also showed that ecosystem C started to recover at 14 years of age in a chronosequence of Douglas-fir (*Pseudotsuga menziesii*) stands after clearcut harvest. However, NEP in this study became much smaller in 2009 than in 2008 for each studied plantation. The decline in NEP could be attributed to the much drier and warmer weather in the growing season of 2009 (Grant et al. 2009b), which resulted in a lower NPP and a large R_h. This phenomenon illustrates the strong interannual variability in ecosystem C balance and indicates that in the future climate warming/drought scenario, NEP could dramatically decrease. In order to better understand the warming/drought effects on NEP, further research should focus on simulating warming/drought scenarios in the field to test their effects on ecosystem C balance. The finding that NEP increased with stand age implies that within the rotation (20-25 years), the older plantations have a greater capacity to sequester more carbon. In order to know when the plantations have the maximal C sequestration capacity, the NEP should be assessed annually.

However, 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. First, the decomposition of severed roots within the trenched plots may contribute to heterotrophic respiration. Secondly, the roots of the understory vegetation could also have contributed a large portion of the so-measured heterotrophic respiration. And third, the trenched plots may have more soil water available for microbial activities due to reduced transpiration rates. In addition, understory biomass was not assessed in this study which might contribute to net ecosystem productivity, especially in the younger plantations with an open canopy, even though the understory vegetation was vigorously controlled in the younger plantations as part of the plantation management regime. At last, when NEP was calculated, the root litterfall which can account for part of the NPP (Steinaker and Wilson 2005) was not included due to the difficulty in collecting root litterfall. Therefore, if both the understory biomass and root litterfall was considered in calculating the NEP, C neutrality would have occurred earlier.

5. Conclusions

Similar diurnal and seasonal variations of soil respiration were found in the different aged plantations in any given year, with significant interannual variation found for each stand age. Soil temperature explained most of the seasonal variation in 2008, a year with non-limiting soil water content. We conclude that air/soil temperature was the major control on soil respiration rates and that relationship was not affected by stand development within the range of stand ages we studied. The strong temperature control on soil respiration also resulted in the lack of stand age effect on the seasonal dynamics of soil respiration. Different time lags were observed between diurnal variation of soil respiration and soil temperature in the different aged plantations and in different years. This has implication for scaling up point soil respiration measurements (such as those using a static chamber system) to seasonal or annual soil respiration values. In general, soil respiration and NPP increased with stand age but NPP increased at a faster rate than heterotrophic respiration, resulting in increased NEP with stand age. Our research indicates that ecosystem C balance has strong interannual variability and is vulnerable to changing climatic conditions. Future research should focus on calibrating or developing site specific below ground biomass equations for older plantations to improve the accuracy of *NPP* calculations and improve the methods for determining heterotrophic respiration rates. With those improvements, more precise *NEP* calculations will be possible.

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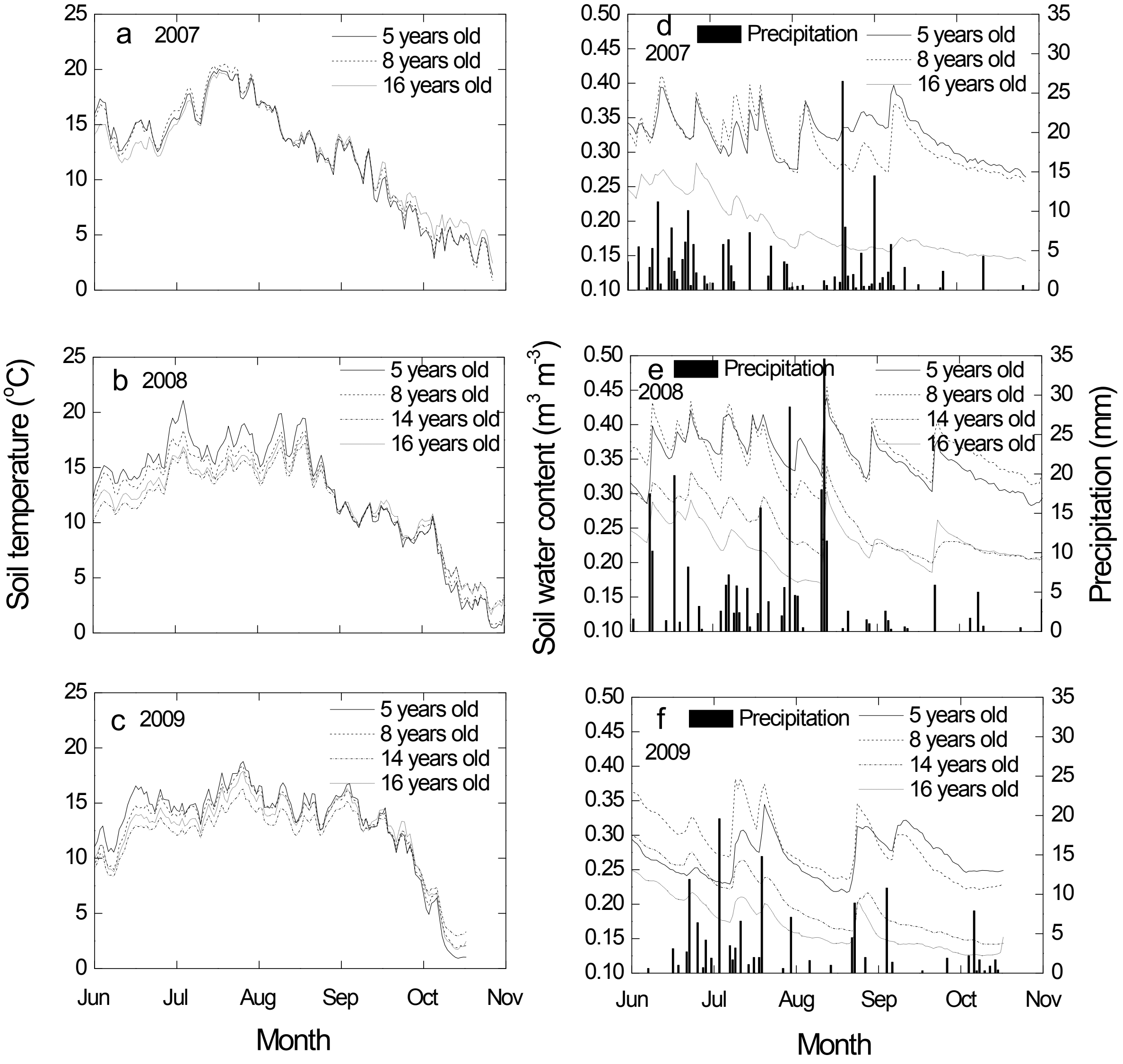

Figure 3 - 1. Seasonal dynamics of daily mean soil temperature at 10 cm depth from June to November in (a) 2007, (b) 2008 and (c) 2009 and soil water content at 10 cm depth from June to November in (e) 2007, (f) 2008 and (g) 2009 for the different aged hybrid poplar plantations.

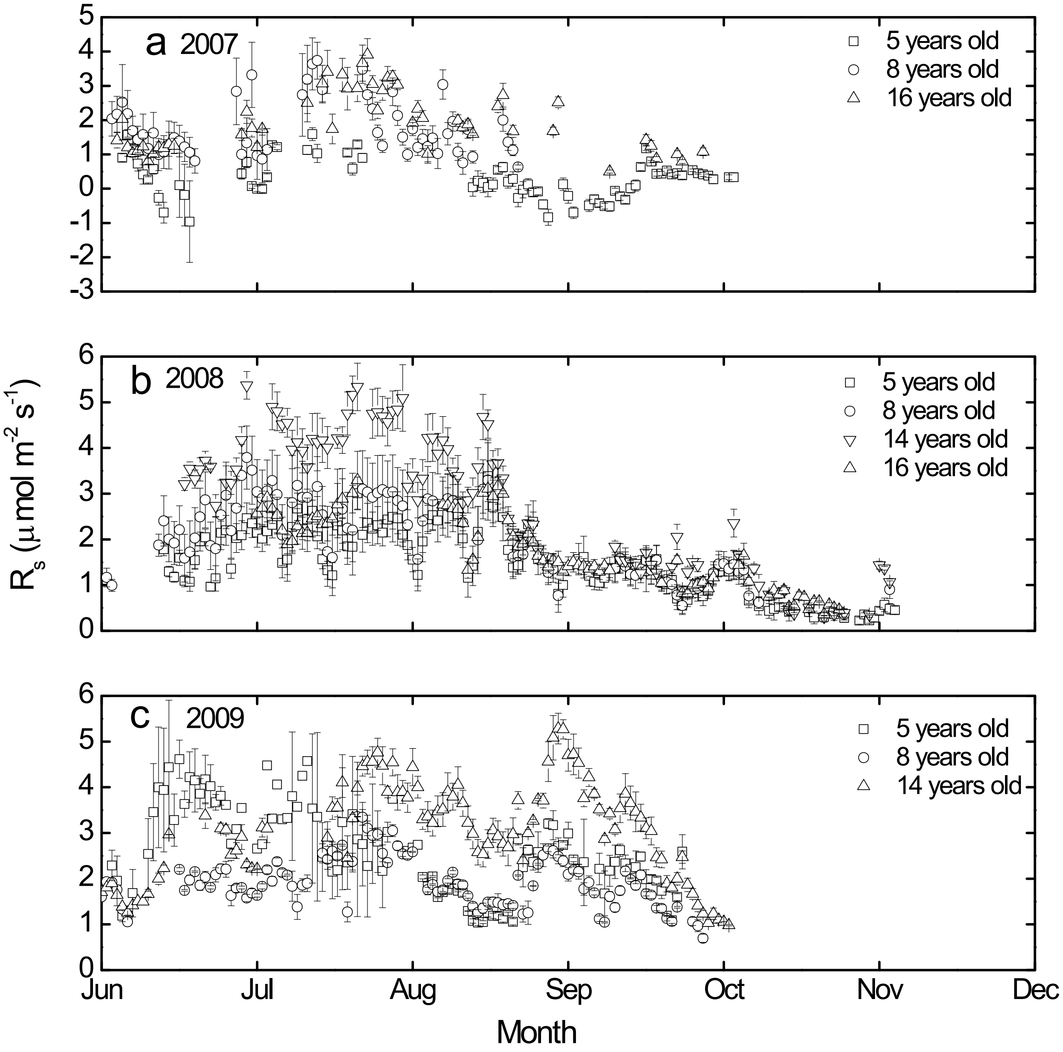

Figure 3 - 2. Seasonal course of daily mean soil respiration (R_s) (a) from June to early October in 2007, (b) from June to November in 2008 and (c) from June to early October in 2009. Note that soil respiration measured in 2007 with the contribution of understory vegetation in the chamber, while understory vegetation was removed in 2008 and 2009 when soil respiration was measured (the same below).

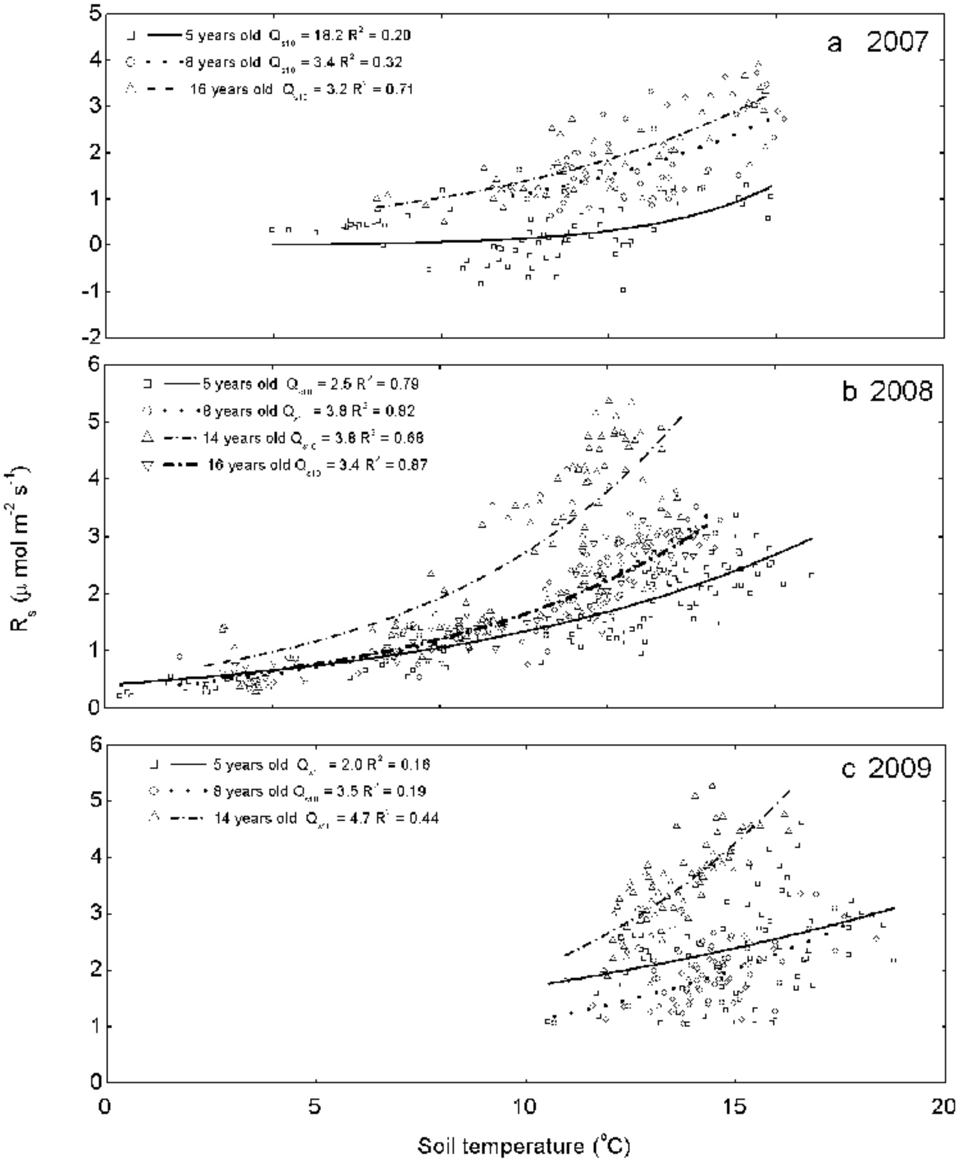

Figure 3 - 3. Relationship between daily mean soil respiration (R_s) and daily mean soil temperature (T_s) at 10 cm depth in different plantations in (a) 2007, (b) 2008 and (c) 2009.

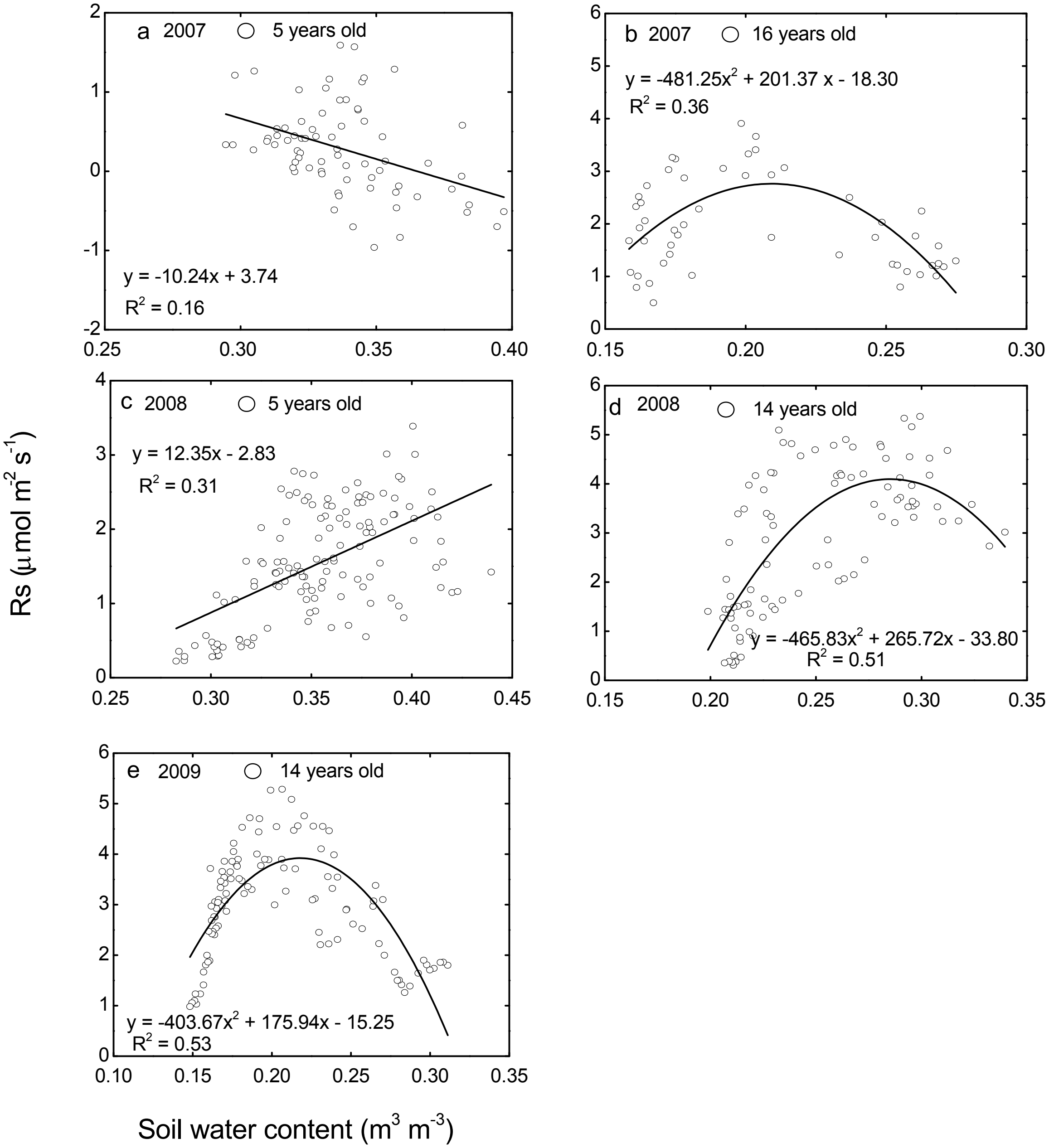

Figure 3 - 4. Relationship between daily mean soil respiration (R_s) and daily mean soil water content at 10 cm depth in different plantations.

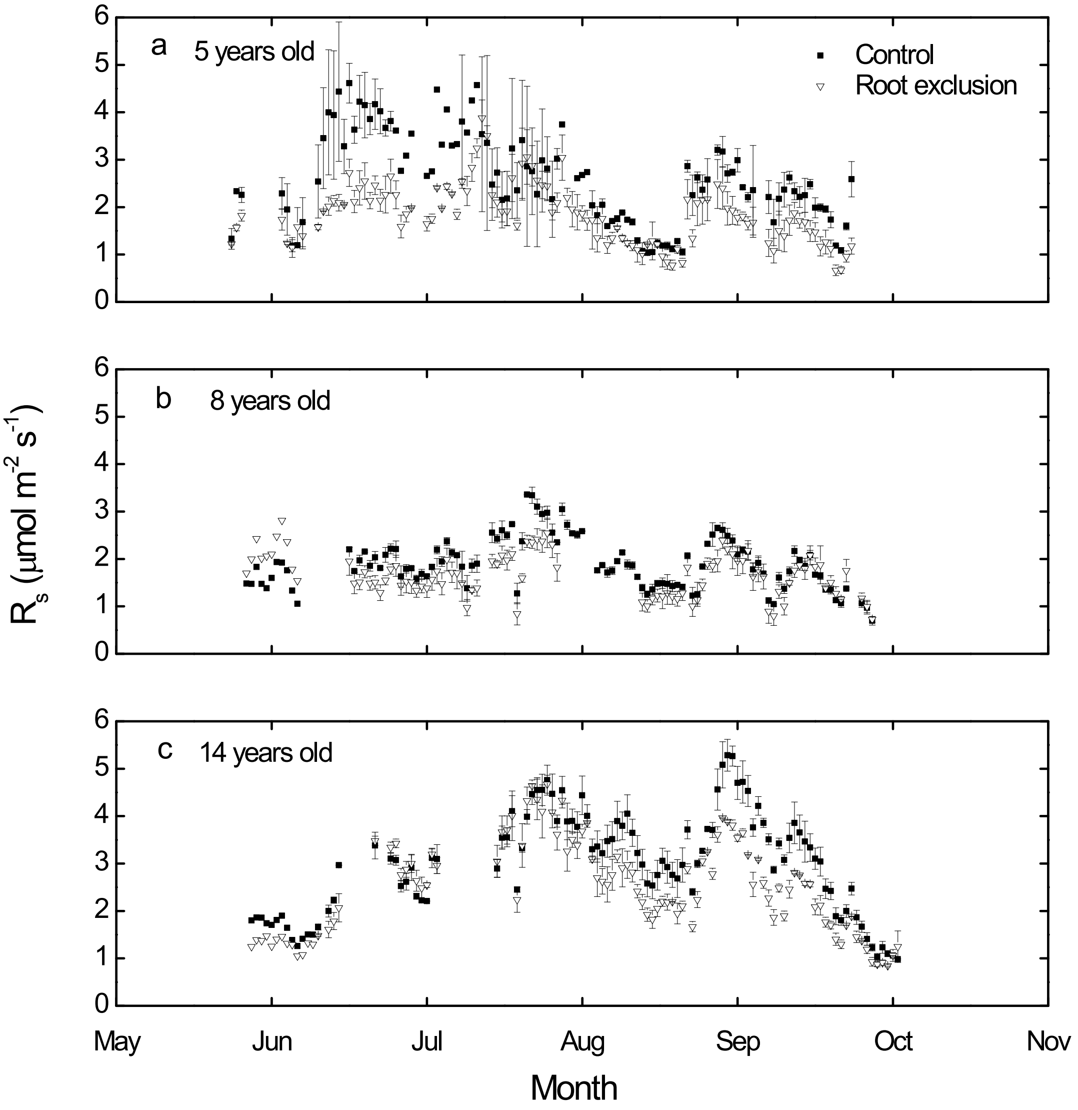

Figure 3 - 5. Seasonal variation of soil respiration in both control and root exclusion treatments in different plantations from June to early October in 2009.

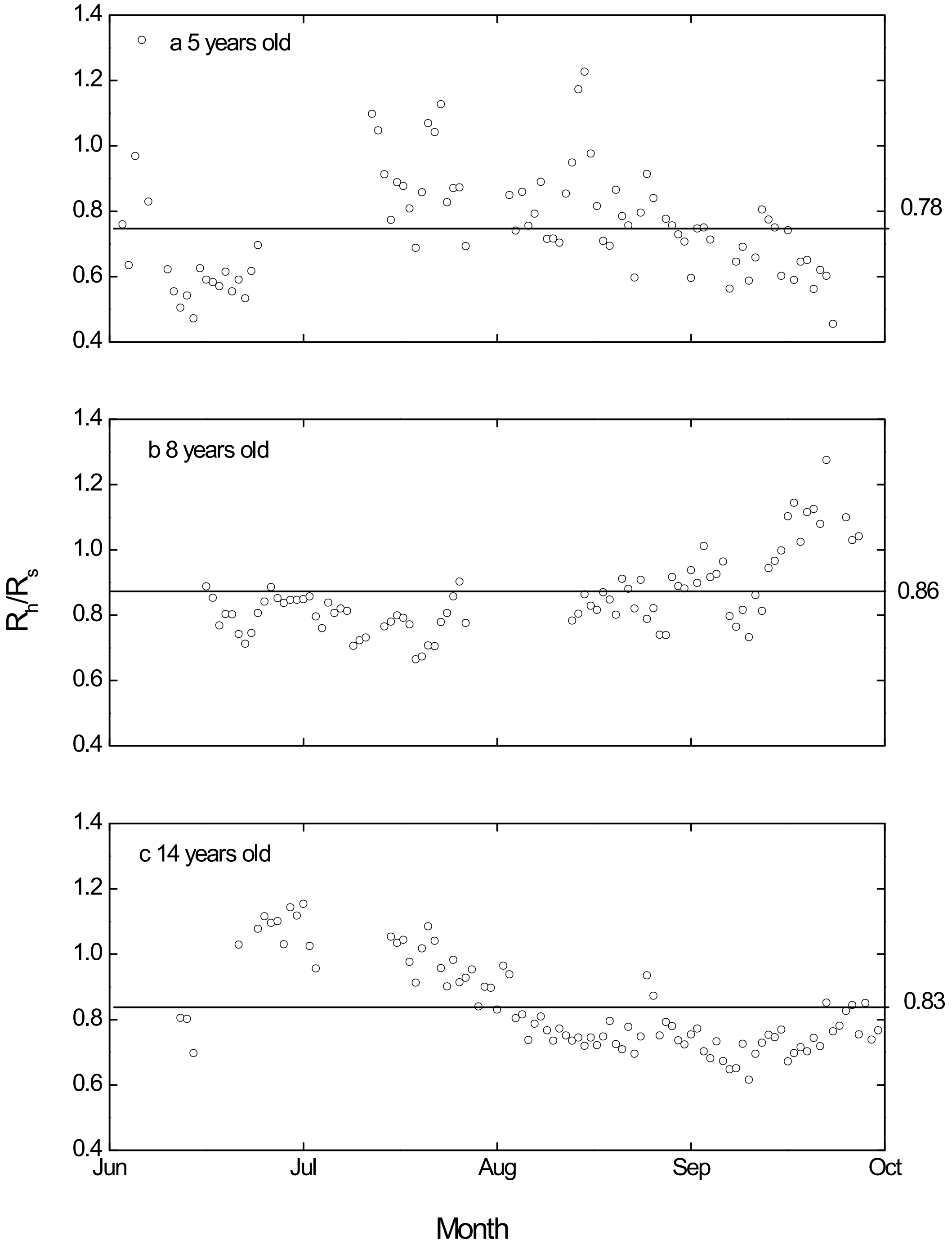

Figure 3 - 6. Seasonal variation of R_h:R_s ratio in different plantations from June to early October in 2009.

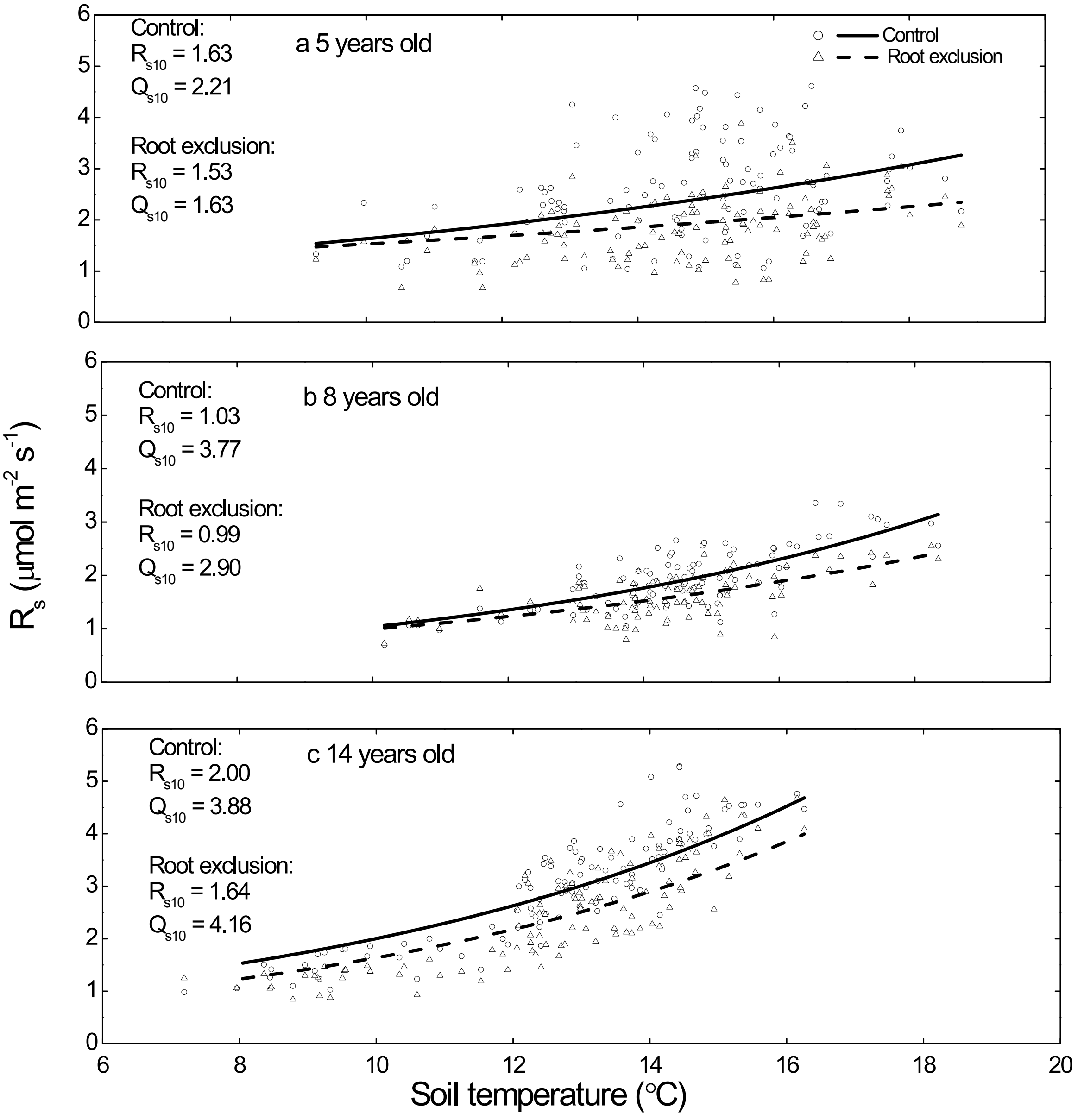

Figure 3 - 7. Relationship between daily mean soil respiration (R_s) in control and root exclusion treatments and daily mean soil temperature (T_s) at 10 cm in different plantations in 2009.

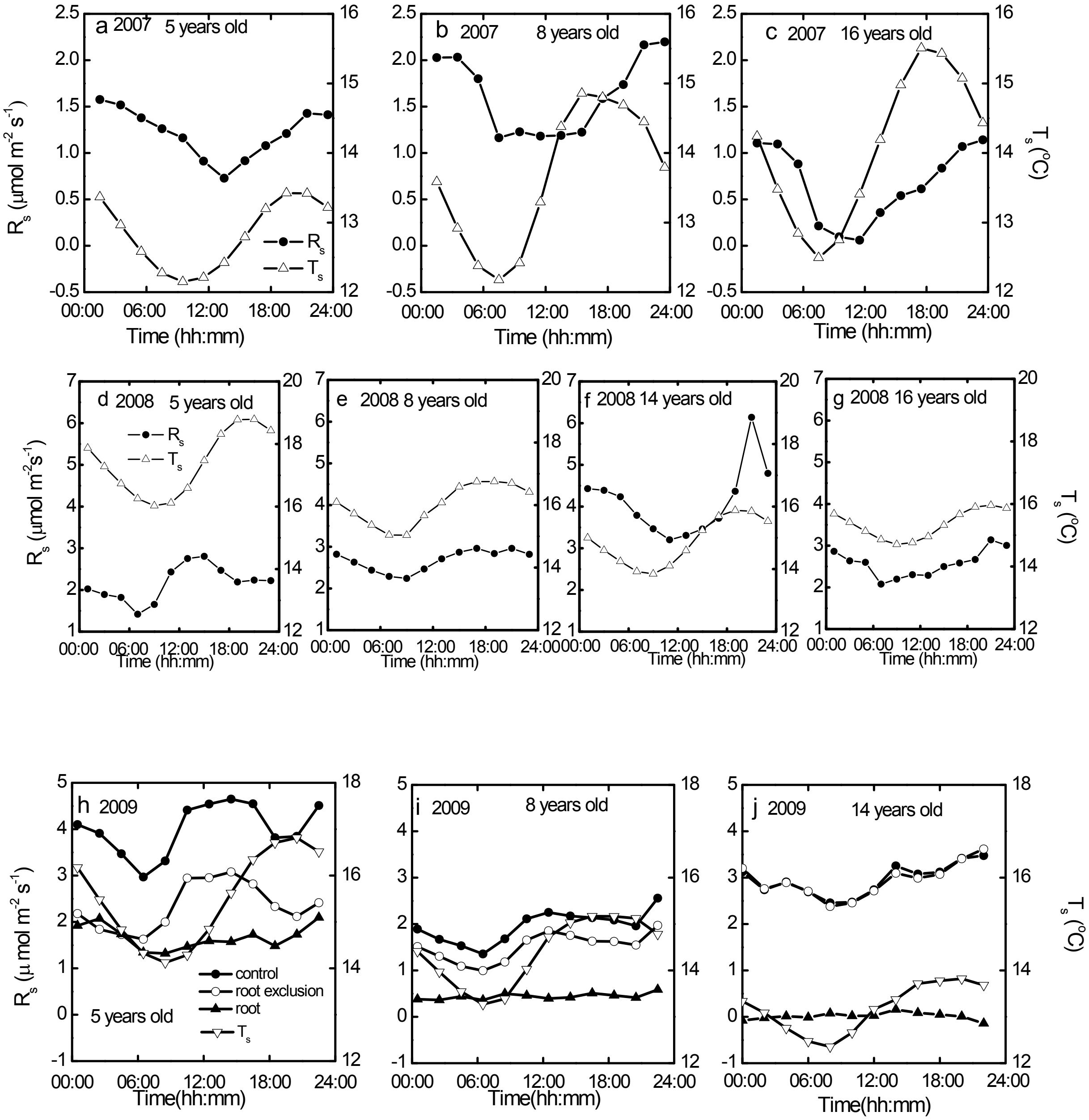

Figure 3 - 8. Diurnal variation of bihourly mean soil respiration (R_s) and bihourly mean soil temperature (T_s) at 10 cm depth in different plantations in 2007 (July 5 to 12), 2008 (July 14 to August 12), and 2009 (June 16 to 28).

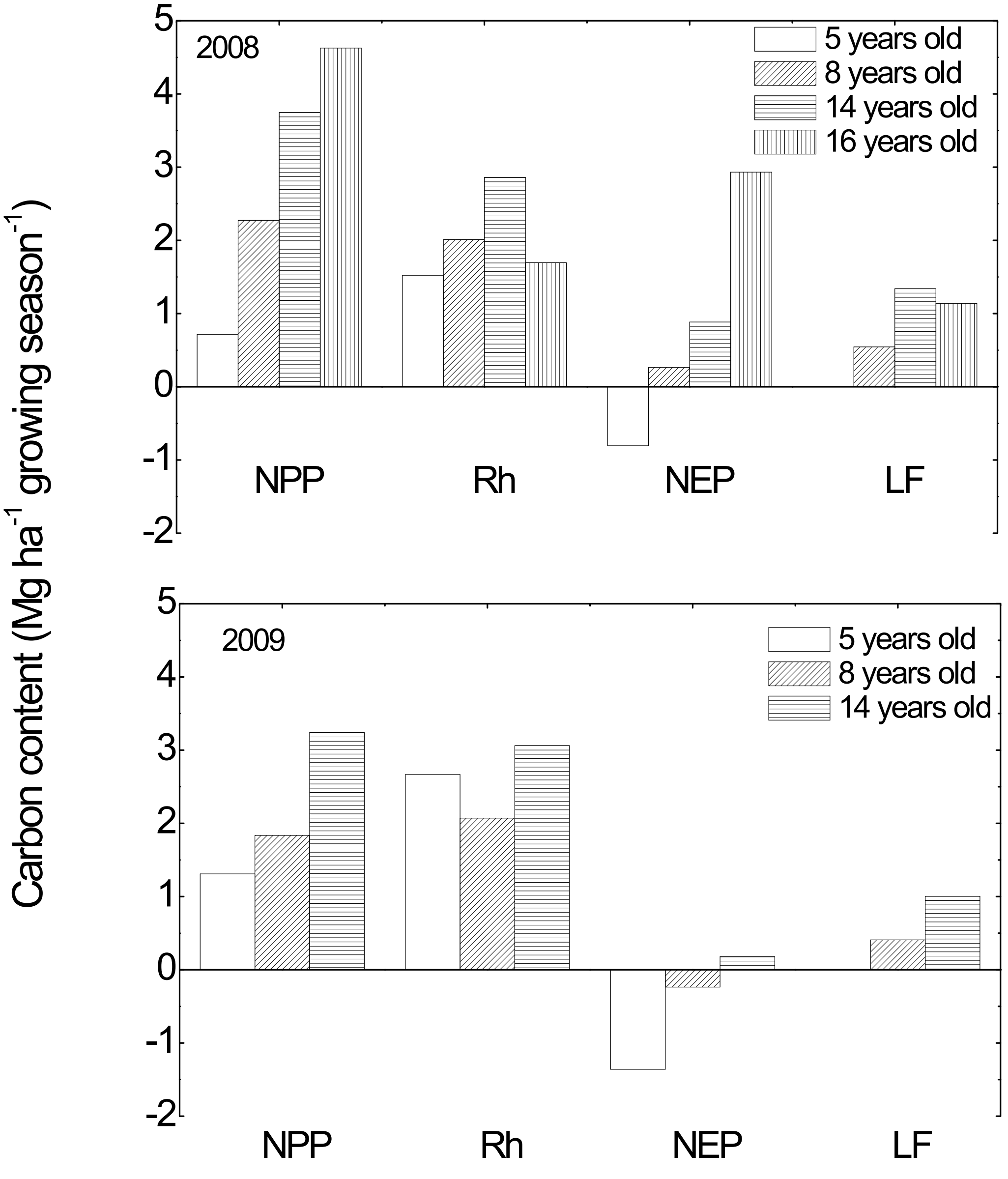

Figure 3 - 9. Net primary productivity (NPP), heterotrophic respiration (R_h) and net ecosystem productivity (NEP) throughout the growing season in different plantations in 2008 and 2009

Chapter 4 Modelling carbon dynamics in hybrid poplar plantations under contrasting soil conditions through the first rotation

1. Introduction

There is a growing interest in planting highly productive, intensively managed plantations such as short rotation hybrid poplars in Canada to supply fibre to the pulp and paper industry (Samson et al. 1999). Also, this productive forestry practice can help sequester more CO_2 from the atmosphere than can native northern forests. In Canada, the provincial government of Saskatchewan announced plans to convert about 1.6 million hectares of marginal agricultural land into tree plantations over the next 20 years by primarily planting hybrid (Haverstock 2005). Alberta-Pacific Forest Industries Inc. (Al-Pac) in Alberta has the goal of leasing 1200 hectares of land annually for planting hybrid poplars on marginal agricultural land in north-central Alberta. Their goal is to establish 25,000 hectares of hybrid poplar plantations by 2020. In British Columbia and Ontario, systems for planting and breeding hybrid poplars have been developed over decades (Welham et al. 2007). This has political and economical impacts, since countries may choose to account for forest management activities to fulfill their commitments under the Kyoto Protocol (Bernstein 2002b). Until now, little research has been conducted to verify the carbon (C) accumulation in hybrid poplar plantations established by forest companies such as Al-Pac, which should be an important part of evaluating C accumulation in Canada's forests.

Net primary productivity (NPP) and net ecosystem productivity (NEP) have been extensively used as indexes to calculate the carbon balance of forest ecosystems over time (Bond-Lamberty et al. 2004b, Howard et al. 2004, Arain and Restrepo-Coupe 2005, Arevalo et al. 2009, Zha et al. 2009). The NPP and NEP of forest ecosystems can be significantly affected by soil conditions such as nutrient and water availability (Grant et al. 2007a). Nutrient availability is expected to be severe in soils with low soil organic matter content and corresponding low soil nitrogen content (Welham et al. 2007), given that soil nitrogen is often the most limiting nutrient in the boreal forest region. Limitations in water availability are also expected in coarse-textured soils that have low water holding capacity and rapid drainage (Grant et al. 2007a). Welham et al. (2007) made projections on boreal poplar total biomass production over a 20-year rotation based on data collected from three different types of soils (poor, medium and rich soils) in Saskatchewan and found that the rich soil had the best tree growth. The poor and rich soils in the Welham et al. (2007) study differed in terms of soil organic matter (SOM) and total nitrogen (N) content in the top 60 cm, with 160 and 7 Mg ha^{-1}of SOM and N in the rich site and 70 and 4 Mg ha^{-1}of SOM and N in the poor site.

Several ecosystem models have been used to predict forest ecosystem NPP and NEP as they were affected by climate change, soil condition, stand age and disturbance (Kimmins et al. 1999, Seely et al. 2002, Grant et al. 2007b, Welham et al. 2007). An ecosystem model, *ecosys*, has been used to project NPP and NEP over the entire rotation of forests to provide verifiable C values for the rotation (Grant and Nalder 2000, Grant et al. 2003, Grant et al. 2007b, Grant et al. 2009a). *Ecosys* has been successfully applied to many native forests, especially boreal forests and even tundra to model changes of NPP and NEP under many different climate scenarios, e.g., drought and warming (Grant et al.

1999, Grant et al. 2001, Grant et al. 2003, Grant et al. 2005, Grant et al. 2007b, Grant et al. 2009a).

The reliability of *ecosys* has been tested many times. For example, Grant and Nalder (2000) modelled long-term carbon accumulation in a boreal aspen-hazelnut forest over 120 years using *ecosys* and found that the modelled average rate of carbon accumulation of aspen wood was slightly lower than that measured from different aged aspen stands in central Alberta and Saskatchewan. Grant et al. (2006) tested the negative effect of drought on NPP and NEP in a boreal aspen forest using *ecosys* and found agreement between modelled and calculated data on these two variables; they proposed that drought would increase leaf stomatal resistance and hence limit CO_2 fixation, and *ecosys* could model the drought effect with soil-root-canopy hydraulic resistance scheme coupled with a canopy energy balance closure scheme. The above hypothesis could be applicable to hybrid poplars, considering that aspen in the study of Grant et al. (2006) and hybrid poplar in the current study are both broad-leaved deciduous trees and the aspen could therefore be used as an analogue for hybrid poplars. In another example, Grant et al. (2009b) simulated interannual changes in seasonal variation of NEP with climate warming, with a rise in NEP in spring, and declines in summer in three boreal black spruce stands in Saskatchewan, Manitoba and Quebec. In their study, they hypothesized that the increase in NEP in spring could be attributable to the early recovery of photosynthetic capacity; the decrease in NEP in summer was caused by the decreased canopy stomatal conductance in late afternoon under high vapour pressure deficit.

However, *ecosys* has not been used to project C dynamics in managed plantations, particularly short-rotation hybrid poplar plantations. In addition, the effect of soil conditions on carbon dynamics in these short-rotation plantations have not been modelled with *ecosys*. In this study, we used *ecosys* to model carbon dynamics in both wood and soil of hybrid poplar plantations under contrasting soil conditions over a rotation (20 years). Our objective was to project C dynamics in hybrid poplar plantations under contrasting soil conditions over the first rotation after being established on previously agricultural lands.

2. Model Structure

A detailed description of model algorithms and parameters of the *ecosys* model can be found in Grant (2001). A brief description of the algorithms used in the *ecosys* model to simulate the effect of soil conditions on carbon accumulation in the hybrid poplar plantations is given below:

2.1. Gross primary productivity (GPP)

Gross primary productivity is determined by carboxylation and CO_2 diffusion (Grant et al. 1999). Carboxylation is controlled by irradiance, leaf temperature, and leaf CO_2 concentration. The CO_2 diffusion is controlled by the CO_2 concentration gradient between leaf and atmosphere, and leaf conductance. The initial leaf carboxylation rate is calculated under a maximum leaf conductance with ambient irradiance, canopy temperature and atmospheric CO_2 concentration. After sequential convergences for canopy temperature and water potential from sequential closures of the canopy energy and water balances, leaf carboxylation rate is recalculated under the ambient conductance at which the diffusion rate of gaseous CO_2 between the atmosphere and leaf equals the carboxylation rate at the mesophyll CO_2. The algorithms used to calculate GPP are detailed in Grant et al. (2001 and 2006).

2.2. Autotrophic respiration (Ra)

The products of CO_2 fixation are stored in non-structural C pools in each branch. Some of them are also moved down concentration gradients to non-structural C pools in root layers. Autotrophic respiration is the sum of all the C oxidized for plant maintenance (maintenance respiration) and growth (growth respiration), using a first-order function of storage C (Grant et al. 2006). If the oxidation of this non-structural C cannot meet the maintenance respiration requirement, remobilizable C from twigs and leaves would be consumed causing litterfall of associated structural C. If the amount of non-structural C exceeds the maintenance respiration, then the excess is used for growth respiration to form new biomass. The details of the algorithm used to calculate Ra are described in Grant et al. (2001 and 2006).

2.3. Nutrient uptake

Mass flow and diffusion of [NH_4+], [NO_3-] and [H_2PO_4-] from soil solution to root and mycorrhizal surfaces equals uptake rate of N and phosphorous (P) by the surfaces. The N and P concentrations in the soil solution are controlled by precipitation, adsorption, solute transport and microbial activity such as mineralization, nitrification and denitrification. Products of N and P uptake are stored in non-structural pools for translocation to growing organs. The details of the algorithm used to calculate uptake are provided in Grant et al. (2001 and 2007a).

2.4. Plant growth

Growth respiration drives plant growth through mobilization of non-structural C, N and P based on phenology-dependent partitioning coefficients and biochemically based growth yields (Grant 2001). The growth of shoots, roots and mycorrhizae requires the transfer of non-structural C, N and P, driven by concentration differences arising from uptake vs. consumption of non-structural C, N and P in different plant organs. Low non-structural N: C or P: C ratios in branches indicate that the N or P uptake, rather than C fixation, is constraining branch growth. These low N: C or P: C ratios cause smaller concentration gradients of N or P, and larger concentration gradients of C between root and shoot, and results in transfer of more C into roots.

2.5. Heterotrophic Respiration (R_h)

Heterotrophic respiration (R_h) in each soil layer is controlled by concentrations of hydrolysis products (dissolved organic carbon, dissolved organic nitrogen and dissolved organic phosphorous) from 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 et al. 2007b). The CO_2 from R_h is transferred to the soil surface by volatilization and diffusion in gaseous and aqueous phases (Grant et al. 2007a). Grant et al. (2006) provides a detailed account of the calculation of R_h.

3. Methods

3.1. Site description

The study sites were located near the Al-Pac mill site (54°49′N, 113°31′W), in the southern area of the Boreal Mixedwood ecological subregion in northern Alberta, Canada. The climate in this area is continental, with short, warm summers and long, cold winters. The growing season is about 175 – 180 days, from May to October (Government of Alberta, 2006). Mean annual temperature and precipitation in this area are 2.1 °C and 503.7 mm (including snow fall), respectively (Environment Canada, 2004). Aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), white spruce (*Picea glauca* Voss), and jack pine (*Pinus banksiana* Lamb) are the dominant native tree species on uplands in this area (Natural Regions committee, 2006). Level to gently undulating plains is the primary landform and the dominant soil type based on the Canadian system of soil classification (Soil Classification Working Group, 1998) is Gray Luvisol, with Dystric and Eutric Brunisols occurring in areas with coarse textured soils (Natural Regions and Subregions of Alberta, 2006). The experimental area occurs on Gleysolic soil according to Saurette et al. (2008a). This research area had been used for agriculture activities during the latter half of the twentieth century.

Four different aged hybrid poplar (*Populus deltoides* × *Populus* × *petrowskyana* var. Walker) plantations were planted in Field 28 south (tree density: 1111 ha^{-1}) established in 2004, Field 28 north (tree density: 1111 ha^{-1}) in 2001, Field 8 (tree density: 1134 ha^{-1}) in 1995 and Field 1 (tree density: 1667 ha^{-1}) in 1993. The test sites were categorized Field 28 south and north as medium (M) sites, Field 8 as a rich (R) site, and Field 1 as a poor (P) site based on the soil texture and soil organic C and total N contents in each site (Table 2). For convenience, we named the plantations with their soil conditions and ages at 2009. Thus, Field 28 south is named M5, Field 28 north is named M8, Field 8 is named R14, and Field 1 is named P16. All the selected plantations were established on previously marginal agricultural lands and had high variability of soil organic carbon and total nitrogen contents (Saurette et al. 2006, Teklay and Chang 2008). Soil characteristics in these four differently aged plantations can be found in Appendix I and Saurette et al. (2006) and Teklay and Chang (2008).

3.2. Soil respiration (R_s) measurements

Soil respiration was measured using a non-steady state automated chamber system (ACS) from June to early November, 2008, and June to early October, 2009. In the 2008 measurements, each ACS was equipped with three chambers (52.5 cm internal diameter, 50 L volume) with dome-shaped lids. The transparent chamber lids were covered with aluminum foil and aboveground understory vegetation in the chambers was cut every two weeks. In 2009, each ACS was equipped with four chambers, two placed in the control treatment and the other two in the root exclusion treatment. The chambers were closed sequentially for one minute every two hours to measure the rate of soil respiration using an infrared gas analyzer (IRGA, LI810 CO_2/H_2O analyzer). At each measurement time, the CO_2 concentration was determined every second for one minute. The slope of the CO_2 concentration increase was derived using linear regression. Soil respiration was calculated using the following equation:

$$R_s = \rho_a \frac{V}{A} \frac{ds_c}{dt}$$

where ρa is the dry air density in the chamber headspace (mol m^{-3}), V is the chamber volume (0.05 m^3), A is the area covered by the chamber (0.216 m^2), dsc/dt is the change rate of the CO_2 mixing ratio in the headspace over the measurement time. The lids were kept open when the chambers were not in use to allow rain, and litter to fall into the collar area.

Approximately 15% of the soil respiration data across all the plantations were lost due to poor power supply during rainy or cloudy days or to improper closure of the chambers (such as when a fallen twig prevented the proper closure of a chamber lid). The CO_2 concentration was recorded every second and increased linearly during the one-minute closure. Data with acceptable slopes of increased CO_2 concentration were retained for analysis. As long as the linear regression was significant, the slopes were accepted.

3.3. Heterotrophic respiration (R_h) measurements

In order to directly measure heterotrophic respiration, two root-exclusion and two control plots (1 x 1m) were established in each plantation in late May of 2009. The root-exclusion plots were set up by trenching soil to 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. The trenched walls were lined with a polypropylene landscaping fabric, which allowed water to go through but excluded roots from penetrating into the trenched plots. Trenches were backfilled with excavated soil. The control plots with no trenching were established adjacent to the root-exclusion plots in the same tree row.

Mean heterotrophic respiration (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. (2008b) for four different aged hybrid poplar plantations in the same area as our study. In 2009, a trenching method was used to measure R_h using the ACS system. In order to account for the CO_2 efflux caused by decomposition of severed roots in creating the trenched plots, a correction factor of 0.83 as determined by Saurette et al. (2008b) was used. Mean R_h throughout the growing season in 2009 was calculated using mean soil respiration in the trenched plots multiplied by the correction factor.

3.4. Aboveground biomass (AGB), NPP and NEP estimation

A 15 x 15 m plot 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 each growing season. Oven-dry AGB (in kg) was derived using the following equation:

Oven-dried AGB = 0.6298 * DBH 1.3582*H 0.2353

This equation was developed for Walker poplar in the same study area by Saurette et al. (in preparation).

Root biomass for the two younger plantations was calculated using the equation established by Saurette et al. (in preparation):

Oven-dried root biomass (RB) = 1.1810 * DHB2.5123*H-2.1616

Root biomass (RB, kg) for the two older plantations was calculated as follows (Fang et al. 2007):

Oven-dried root biomass (RB) = EXP (3.97-252.92 / (DBH*H))

The equations developed by Saurette et al. (in preparation) for both aboveground and root biomass were based on the data from 8-year-old Walker poplar. Comparing aboveground biomass calculated from the equation of Saurette et al. (in preparation) to that developed by the Ontario Ministry of Natural Resources (1991) which includes a wide range of DBH of hybrid poplars, showed no significant difference. In terms of choosing the root biomass equations, when the equation of Saurette et al. (in preparation) was used to calculate the trees from the two younger plantations, the ratio between aboveground and root biomass was similar to what Fang et al. (2007) found for younger plantations; when the root equation of Fang et al. (2007) was used for the two older plantations, the ratio between the aboveground and root biomass was close to what Fang et al. (2007) found for older plantations.

For determining above-ground litterfall rates, 13 round buckets (diameter: 30 cm) were randomly distributed in each plot to collect above-ground litterfall (AGLF). The collected AGLF was oven-dried at 65 °C until constant weight and weighed in the lab. The carbon content in aboveground biomass, root and AGLF was calculated by multiplying a standard factor of 0.5 (Pregitzer and Euskirchen 2004). The NPP equals the biomass carbon increment from the beginning to the end of the growing season, plus above-ground litterfall.

NPP = (AGB + RB) end of growing season - (AGB + RB) beginning of growing season + AGLF

The NEP is the biomass carbon increment of the whole ecosystem which can be determined using the following equation: NEP = NPP- R_h.

4. Model runs

Ecosys was initialized with the soil and topographic properties of the four plantations (Tables 4-1 and 4-2). The daily weather data including daily maximum air temperature, daily minimum air temperature, wind speed, precipitation, relative humidity and solar radiation from 2004 to 2009 were obtained from the nearest weather station (Rich Lake, 54.5° N, 116.6°W)to our site belonging to AgroClimatic Information Service (ACIS), Government of Alberta. *Ecosys* was run for 50 years with spring wheat using 2007 weather data, representing the land use history before planting with hybrid poplars, to spin up the model. Thereafter, *ecosys* was planted with Walker poplar and run for 20 years (a rotation term) under repeated weather data from 2004 to 2009. Perennial grass was planted with the trees to simulate the understory vegetation. The perennial grass shared the same attributes for CO_2 fixation and C allocation by C3 perennial species with the Walker poplar, except that all above-ground biomass turned over each year on July 1st in the first five years after the establishment of plantation. The Walker poplar plantations were harvested on 1 June in the last year of the model run.

5. Model tests

Hourly and daily soil respiration modelled for the four plantations with 2008 and 2009 weather data were compared with hourly and daily soil respiration measured in the fields in 2008 and 2009 by comparing pooled standard error of measured soil respiration to the root mean square difference of the regression between modelled and measured soil respiration rates. The AGB, tree biomass, aboveground litterfall (AGLF), NPP, R_s, R_h and NEP modeled over the growing seasons of 2008 and 2009 were also compared to those derived from the biomass equations. The difference in R_s and R_h between models and measurements was assessed by using one sample T-tests. Since no standard error could be calculated for AGB, tree biomass, AGLF and NEP, their uncertainty was not assessed.

6. Results

6.1. Seasonal and diurnal variation of R_s

Modelled seasonal variation of daily R_s was similar to that of measured R_s, which peaked in July or August and declined thereafter (Fig. 4-1). However, there were exceptions. In the 5- , 7-, 13- and 14-year old stands, the measured soil respiration from June to July or August was much greater than the modeled values (Fig. 4-1). A strong correlation was found between modelled and measured R_s, except in the 6- and 7-year old stands (Fig. 2). The RMSEs in the measured soil respiration were always greater or not different from RMSDs of the regression (Fig. 4-2).

Diurnal variation of modelled R_s was similar to that of measured R_s, taking R_s during DOY 220 – 230 in 2008 and DOY 230 – 240 in 2009 as examples (Fig. 4-3). In both periods, rainfall events occurred. The diurnal pattern of R_s was well modelled in 2008. The sudden decrease and increase in soil respiration during DOY 224 – 226 in 2008, was most likely caused by rainfall effects on soil respiration and was successfully simulated in all the plantations (Fig. 4-3). However, during DOY 234 – 236 in 2009, the rainfall effect on soil respiration was not as evident as in 2008.

6.2. Aboveground biomass (AGB) carbon

The aboveground biomass modelled for 2008 and 2009 in M5, M8, R14 and P16 was similar to that calculated using the aboveground biomass equation (Fig. 4-4). The measured aboveground biomass in P16 was smaller than that in R14, even though the trees in the P16 plantation are older than in R14. This phenomenon could be attributed to poor water holding capacity and nutrient availability in P16 (Table 4-2, Fig. 4-5), and the model successfully simulated this poor growth in P16. The leaf N: C ratio in the R14 was the largest, followed by M5 and M8, and P16 due to the greater soil organic matter content in R14; the minimum canopy water potential in M5 and M8 was greater than that in R14 and P16 due to the older stand age in R14 and P16; the minimum canopy water potential in R14 was larger in 2008 than in 2009 due to the dry weather in 2009 (Fig. 4-5).

6.3. NPP, aboveground litterfall (AGLF), R_s, R_h and NEP

Modelled NPP were greater than estimated in all plantations and in both years, except in P16 in 2008 (Table 4-3); measured NPP was greater in 2008 than in 2009 in the two older plantations (R14 and P16) ; modelled AGLF was always greater than measured in the younger plantation (M8) and similar to that measured in the two older plantations; no significant difference between modelled and measured R_s was observed in most of the plantations in both years, except in R14 in both years, M5 in 2009; modelled R_h was different from estimated R_h in M5 and R14, and no difference was found between them in M9 and P16; no similar relationship between modelled and estimated NEP was observed.

6.4. Carbon dynamics over the first rotation

In the model outputs, the amount of aboveground biomass produced over the rotation (20 years) was in the following order: R14 > M5 and M8 > P16 (Fig. 4-6). Aboveground biomass increased slowly during the first few years of the rotation and then quickly increased for the rest of the rotation for all the plantations mainly due to the low leaf area index for the first a few years of tree growth. For the first four years, trees in P16 grew the fastest due to less competition in P16 compared to other stands, followed by those in R14 and M5 and M8. Then trees in R14 grew the best for the rest of the rotation, when weed competition was not a limiting factor any more. Trees in M5 and M8 outgrew those in P16 at approximately age 14.

The largest NPP and NEP modelled for M5, M8, R14 and P16 were at age 15, 4 and 3, respectively (Fig. 4-7), which might signify that trees growing in M5 and M8 might be greatly affected by the weeds, because the weed biomass in M5 and M8 in the first few years was much greater than in R14 or P16 (data not shown). Smaller inter-annual variation in tree growth and ecosystem carbon accumulation after age five was modelled in P16 than in the other plantations. Large inter-annual variations of NPP and NEP were simulated over the rotation term for M5, M8 and R14. The R14 accumulated the most ecosystem carbon in wood (3700 g m^{-2}), followed by M5, M8 and P16 (Fig. 4-7).

Ninety percent of the aboveground biomass was harvested at the end of the modelled rotation. Soil lost carbon for the first three to five years after plantations were established and then accumulated carbon rapidly for the rest of the rotation (Fig. 4-8). Soils in R14 and M5 and M8 recovered carbon to values at planting, while soils in P16 accumulated much more carbon as compared to values (initial value: 5209 g m^{-2}, end value: 5637 g m^{-2}).

7. Discussion

7.1. Measured and modelled soil respiration

Modelled soil respiration had similar temporal (both diurnal and seasonal) variations to measured soil respiration. This temporal trend could mainly be induced by variation of soil temperature (Davidson and Janssens 2006). The modelled soil respiration was often in agreement with, but sometimes smaller than the values measured with surface chamber systems. Similar results were found by Grant et al. (2006). The measured soil respiration unexplained by the model could be attributable to the uncertainty in the measured ones given that the RMSEs in the measured soil respiration were always greater or not different from the RMSDs of the regression (Fig. 4-2). The uncertainty of the model also existed due to the uncertainty of the inputs (e.g., soil carbon, nitrogen content) caused by spatial variation and sampling methods. Moreover, greater measured soil respiration than modelled for the early growing season in some stands (Fig. 4-1) could also be because the model did not completely simulate the respiration from newly growing fine roots or decomposition of litterfall from previous year.

7.2. Estimated and modelled AGB and NPP under different soil conditions

The aboveground biomass C was overestimated by the model compared to the ones calculated by biomass equations in the medium, younger stands (M5 and M8, Fig. 4-4). The smaller measured biomass C in the first few years after plantations were established could be attributed to the strong weed effect on tree growth (Welham et al. 2007). Weed competition can be the most important limiting factor affecting plantation success (Hansen and Netzer 1985). Weeds compete for water and nutrients with seedlings or young trees in the field and slow the growth of trees. The modelled and calculated aboveground C agreed well with each other in the rich, older site (R14), in which weed competition was weak. However, in the older poor site (P16), modelled aboveground C was slightly smaller than the measured values. We assumed that the smaller tree biomass at the late stage of the rotation in the poor and older site could be attributed to its low nutrient availability at the beginning of plantation establishment (Table 4-2). When weed competition was not a limiting factor to the tree growth at the late stage of the rotation, the nutrient constraint emerged and limited the tree growth in P16.Weed biomass was not assessed in the two older plantations (R14 and P16), which might have caused the greater difference in NPP between modelled and measured NPP in R14 where weeds were abundant (personal observation), while there were few weeds in P16. The smaller NPPs in 2009 than in 2008 in R14 and P16 could be attributed to the drier growing season in 2009 than in 2008, and therefore increased hydraulic resistance could be a limiting factor in the older plantations (Gower et al. 1996) in 2009. In contrast, in the two younger plantations (M5 and M8), NPPs were larger in 2009 than in 2008. It is reasonable considering the higher temperature in 2009 than in 2008 might have resulted in the better tree growth (Grant et al. 2009b) in the younger plantations where the hydraulic constraint might not be a limiting factor for younger trees as in the older plantations (Fig. 4-5). Besides, water constraints might be smaller in young plantations since the transpiration from smaller trees could be lower.

7.3. Carbon accumulation over the first rotation under contrasting soil conditions

The NEPs were negative in the first two years after hybrid poplar was planted on previously agricultural lands, indicating net C loss from the ecosystem (Fig. 4-7). This initial C loss was caused by higher R_h than NPP. The period of initial C loss was shorter than that in some other Canadian boreal forests (Kurz and Apps 1999, Litvak et al. 2003b), probably because coarse woody debris and other residue left at this agricultural site were none, or less than those left after replacing a forest, and rapid early tree growth on fertile agricultural soils. The NPP and NEP reached maximum at different ages on different sites, which might indicate that the effect of weeds and nutrients on tree growth is different on different sites (Welham et al. 2007). Weeds did grow better in the two medium sites for the first few years than in the poor or rich sites (data not shown). Different soil conditions do have significant effects on wood and ecosystem carbon growth. Welham et al. (2007) modelled boreal poplar total biomass over a 20-year rotation based on the data collected from three different types of soils (poor, medium and rich) and found that the rich soil produced the best tree growth. At the end of the plantation rotation, forest soils accumulated carbon in the forms of soil and litter carbon, and recovered the carbon loss in the first few years due to land use change.

Modelled C accumulation rates in wood under different soil conditions were similar to what we estimated based on the field measurements in the current study (Table 4-3, Fig. 4-7). However, comparing to average NPP from age two to nine of Walker poplar plantations measured by Arevalo et al. (2009) in the same eco-region as the current study, average NPP in the rich site (R14) of the current study was much smaller

(430 vs. 700 g C m^{-2} yr^{-1}). The difference could be attributed to the large difference in soil organic matter in their study, especially total nitrogen content, which contained almost twice the nitrogen content of the current study. Modelled soil C in our study increased less from age two to nine compared to what Arevalo et al. (2009) measured (50 vs. 180 g C m^{-2} yr^{-1}), probably due to much greater C inputs from the larger tree growth on their sites.

Many factors in boreal forests can affect the C growth rate. Jarvis and Linder (2000) found that the time between spring thaw and autumn freeze controls the annual tree growth and also determines annual net primary productivity through the temperature effect on CO_2 uptake in spring and nutrient availability and uptake in summer based on long-term observations in boreal forest of northern Saskatchewan and Sweden. Griffis et al. (2003) also pointed out that a warmer climate might favour carbon sequestration in boreal aspen forests. In contrast, summer drought could reduce photosynthetic efficiency and carbon fixation due to declining stomatal conductance and soil water content (Griffis et al. 2003, Grant et al. 2006). In addition, nitrogen is generally considered as the most limiting nutrient in boreal forests, especially in poplar plantations (Guillemette and DesRochers 2008). Application of nitrogen to boreal aspen increased the average carbon storage, mainly in wood products and live biomass (Seely et al. 2002). Therefore, in order to obtain maximal carbon productivity of the hybrid poplar plantations, intensive forest management, e.g., frequency and intensity of weed control, timing and quantity of nitrogen application, and irrigation when drought happens, are necessary. As we found in 2009, a drier year, the drought did affect the tree growth in the older plantation.

8. Conclusions

Soil conditions did affect carbon accumulation in the hybrid poplar plantations, both soil and wood carbon pools. Trees in the rich site sequestered more biomass carbon than in the poor or medium sites. Tree growth in the first few years after plantation establishment was more likely affected by weed growth, and the two medium sites were affected the most while the poor site was affected the least. The NPP and NEP reached maximum at different ages in different soil conditions, at age 15, 4 and 3 for M5 and M8, R14, and P16, respectively. Considering the significant weeds and nutrient effect on NPP and NEP, further model simulation could focus on how NPP and NEP changes over one or more rotations with different weed control management and nutrient application schemes, to further find out which combination could maximize the biomass productivity of these hybrid poplar plantations.

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Table 4 - 1. Climate at and location information of the Al-Pac mill site

Climate and Location	
Latitude (degree)	54.82
Longitude (degree)	113.52
Elevation (m)	626
Mean annual temperature (°C)	2.1
Mean annual precipitation (mm)	503.7
Slope (degree)	0

Note: All climate data from Environment Canada (2004).

Table 4 - 2. Comparisons of soil conditions among P16, R14, and M5 and M8

Soil horizons in cm	LFH (1-0)	Ah1 (0-10)	Ah2 (10-20)	B1 (20-30)	B2 (30-40)	B3 (40-60)	C1 (60-80)	C2 (80-120)	Ck (120-140)
					P16				
Field capacity (m^3 m^{-3})	0.45	0.24	0.24	0.24	0.24	0.23	0.23	0.19	0.18
Wilting points (m^3 m^{-3})	0.15	0.10	0.10	0.10	0.10	0.13	0.13	0.13	0.13
SOC (g Mg^{-1})	430000	14000	14000	7000	5200	3400	2500	2000	2600
Total N (g Mg^{-1})	20199	1300	1300	521	383	317	317	286	200
Sand content (g kg^{-1})	-	623	623	768	768	768	227	227	227
Silt content (g kg^{-1})	-	287	287	166	166	166	499	499	499
					R14				
Field capacity (m^3 m^{-3})	0.45	0.24	0.24	0.24	0.24	0.23	0.23	0.19	0.18
Wilting points (m^3 m^{-3})	0.15	0.10	0.10	0.10	0.10	0.13	0.13	0.13	0.13
SOC (g Mg^{-1})	430000	42000	31000	9400	7800	4500	2500	2000	1500
Total N (g Mg^{-1})	20199	3000	2000	1000	440	340	250	200	150
Sand content (g kg^{-1})	-	520	539	480	454	317	317	317	317
Silt content (g kg^{-1})	-	363	357	400	409	415	415	415	415
					M5 and M8				
Field capacity (m^3 m^{-3})	0.45	0.45	0.45	0.24	0.24	0.23	0.23	0.19	0.18
Wilting points (m^3 m^{-3})	0.15	0.10	0.10	0.10	0.10	0.13	0.13	0.13	0.13
SOC (g Mg^{-1})	430000	27200	24200	9600	5030	3400	2500	2000	2600
Total N (g Mg^{-1})	20199	2720	2420	960	503	340	250	200	260
Sand content (g kg^{-1})	-	194	192	128	93	93	93	93	93
Silt content (g kg^{-1})	-	602	603	641	670	670	670	670	670

Table 4 - 3. Modeled and estimated NPP, AGLF, R_s, R_h and NEP (all units in g C m^{-2}) in 2008 and 2009 in the four test fields. Values a ± b in the Table are means ± standard errors.

Site	M5		M8		R14		P16	
	Modelled	Estimated	Modelled	Estimated	Modelled	Estimated	Modeled	Estimated
Year 2008 (DOY 136-277)								
NPP	325.9	261.2	414.9	402	522.8	374.6	369	462.7
AGLF	/*	/	81.1	54.5	126.7	134.0	94.5	113.7
R_s	294.6	241 ± 24.4	269.1	319 ± 80.4	285.1	454 ± 39.7	279.9	269 ± 30.1
R_h	216.2	151.8 ± 15.4	179.7	201 ± 50.7	191	286 ± 25.0	188.8	169.5 ± 19.0
NEP	109.7	109.4	235.2	201	331.8	88.6	180.2	293.2
Year 2009 (DOY 150-326)								
NPP	363.6	347.5	477	358.2	413	324.4	304.3	227.2
AGLF	/	/	113.9	50.9	107.1	100.5	84.9	85.3
R_s	256.2	404 ± 40.1	330.0	296 ± 35.2	263.6	464 ± 51.7	200.7	/
R_h	168.5	266.6 ± 26.5	185.8	207.2 ± 24.6	181.8	306.2 ± 34.1	126.8	/
NEP	195.1	80.9	291.2	151	231.2	18.2	177.5	/

*: not measured; AGLF: aboveground litterfall

Note: aboveground weed biomass for the younger plantations (M5 and M8) was 174.6 g C m^{-2} (personal communication: Abdul Khaliq). For the two older plantations, aboveground weed biomass was not assessed.

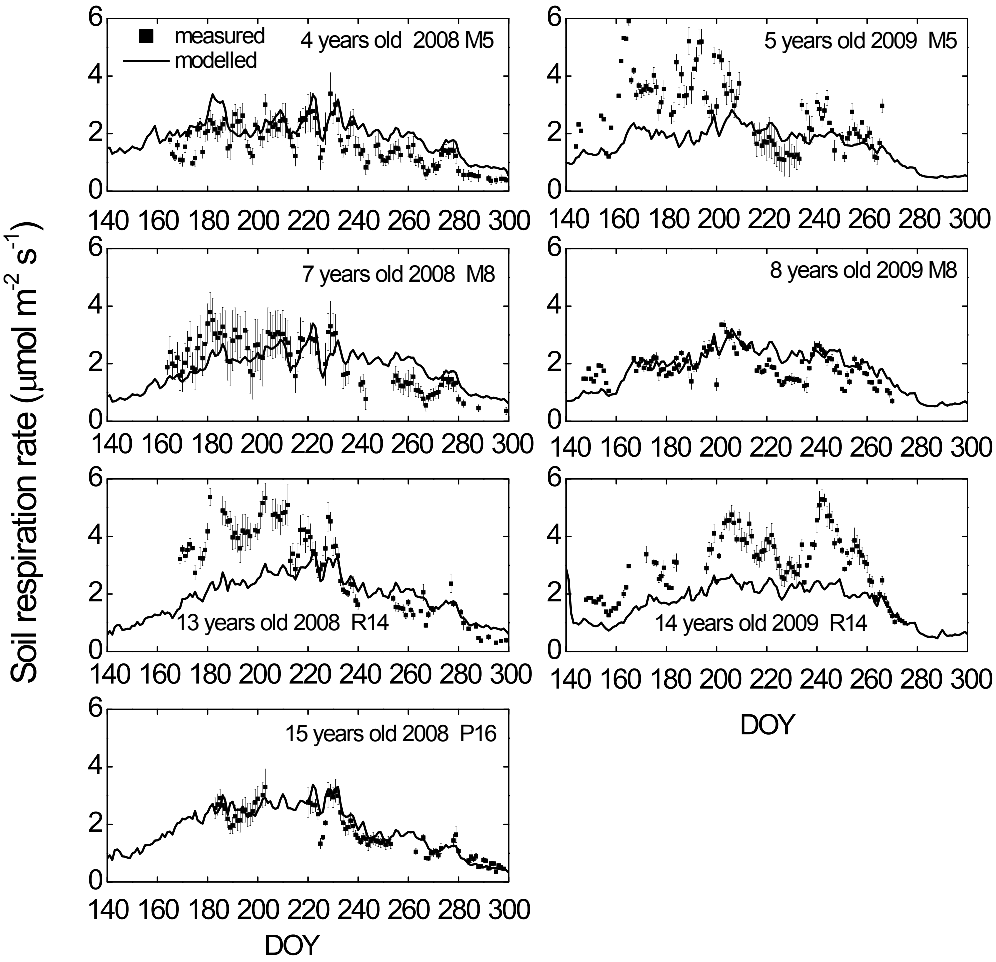

Figure 4 - 1. Measured and modelled daily mean soil respiration in the hybrid poplar plantations during the growing season in 2008 and 2009

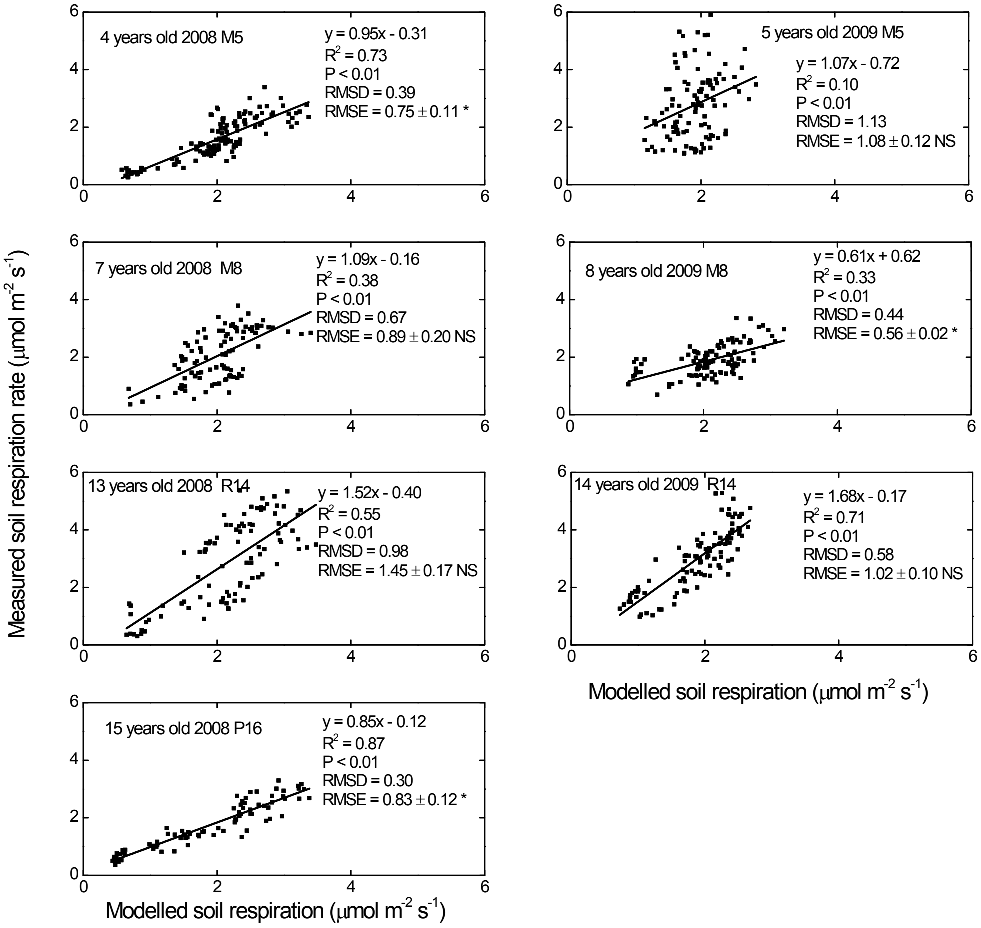

Figure 4 - 2. Regression between measured and modelled daily mean soil respiration in the hybrid poplar plantations (*: indicates RMSE of measured soil respiration is significantly greater than the RMSD of the regression; NS: indicates no significant difference between RMSE and RMSD)

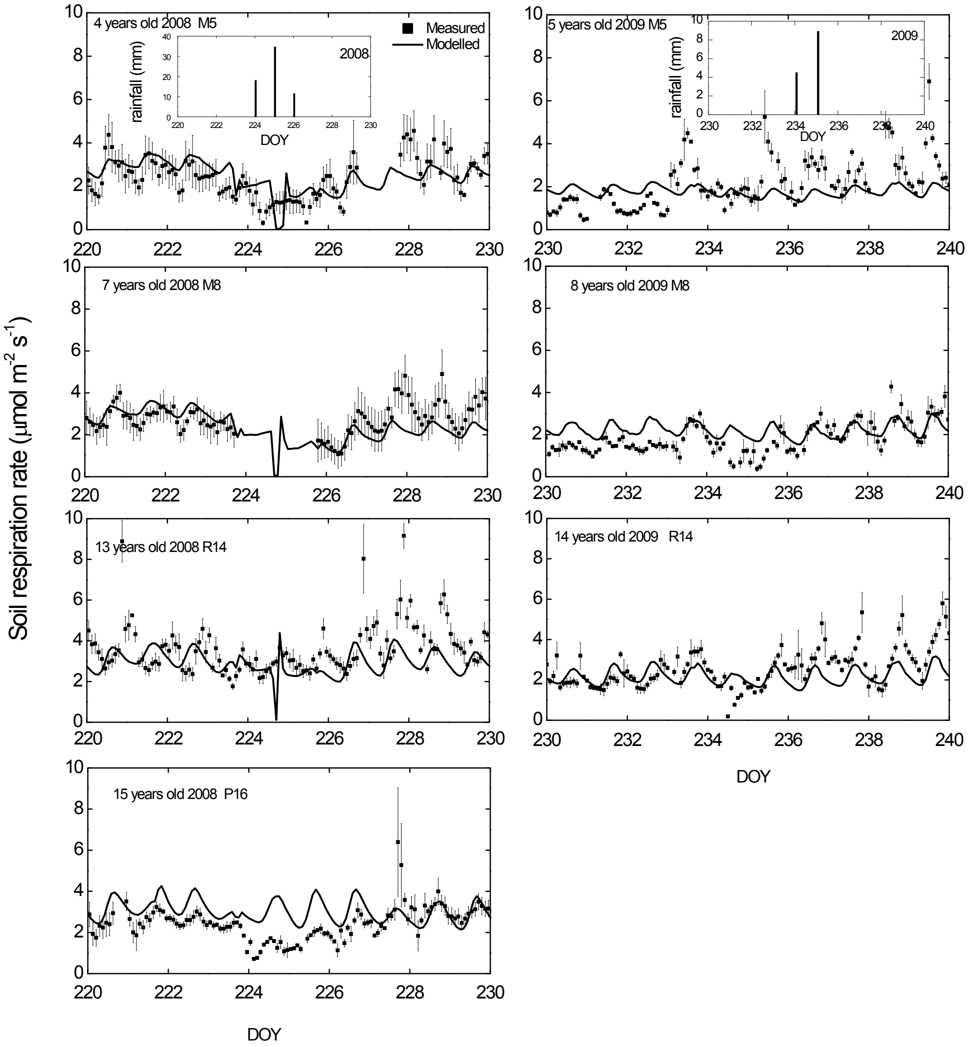

Figure 4 - 3. Measured and modelled bihourly soil respiration in the hybrid poplar plantations during DOY 220 – 230 in 2008 and 230 – 240 in 2009

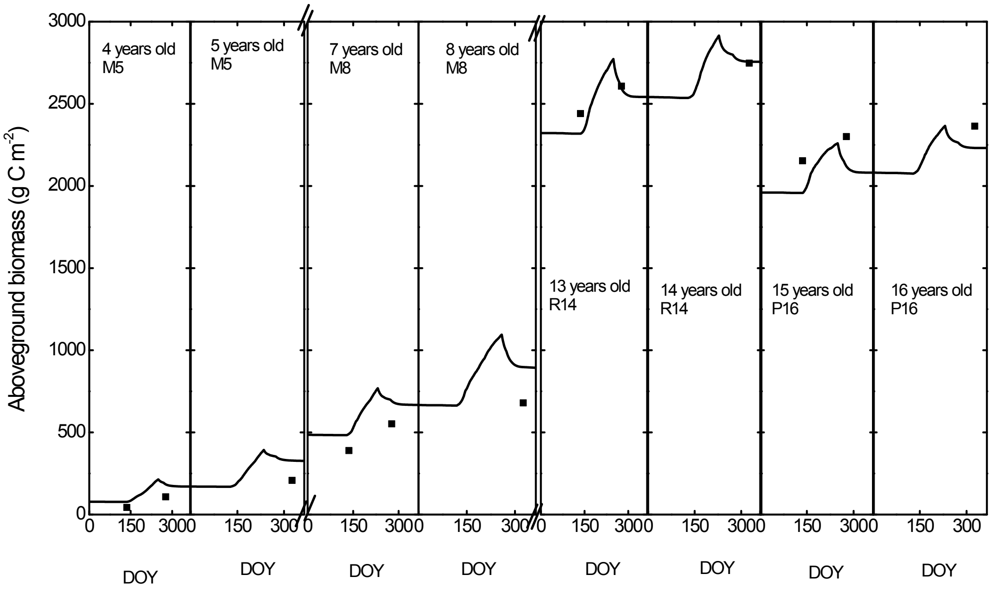

Figure 4 - 4. Measured (dots) and modelled (lines) aboveground tree biomass C in the hybrid poplar plantations in 2008 and 2009

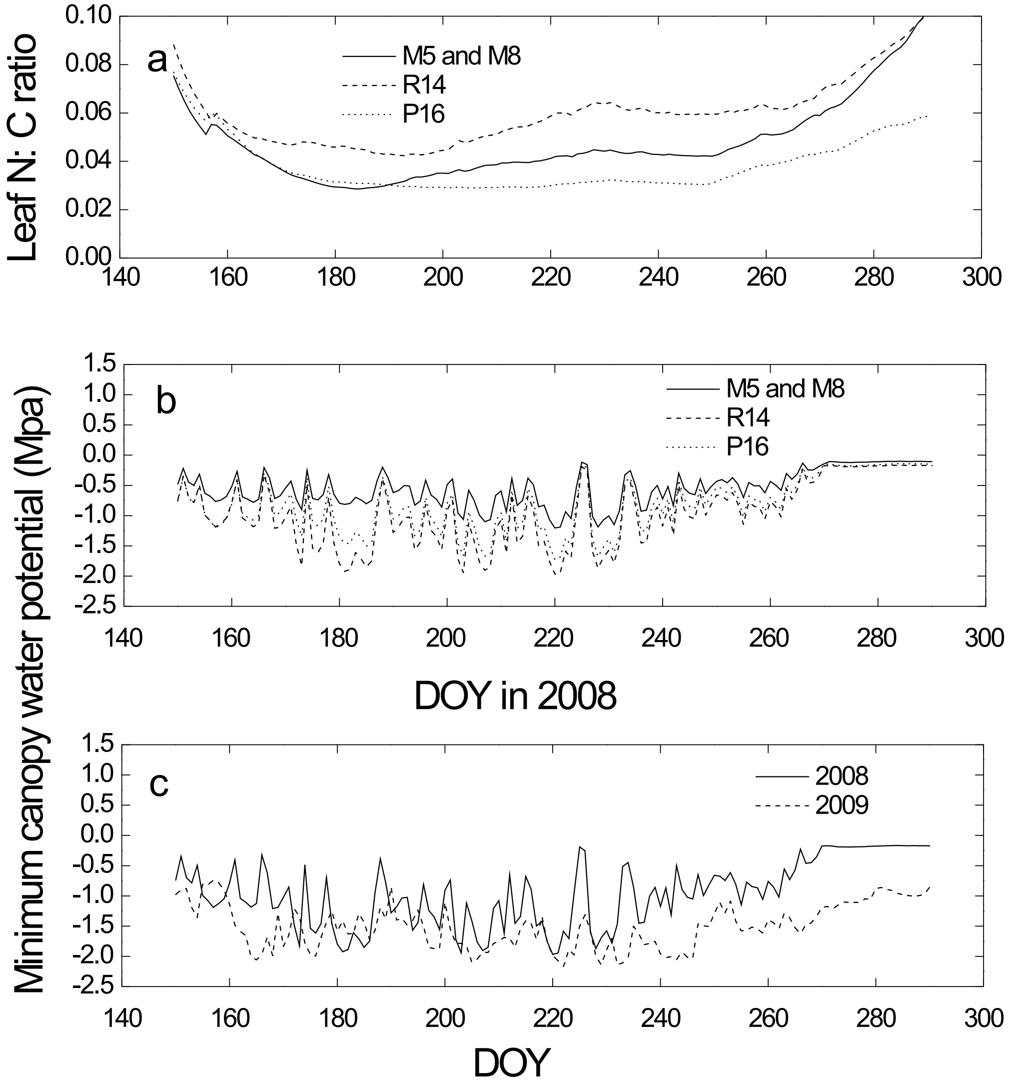

Figure 4 - 5. Model outputs of leaf N: C ratio and minimum canopy water potential in M5 and 8, R14, and P16 from DOY 150 to 290 in 2008 (a and b), and minimum canopy water potential in R14 from DOY 150 to 290 in 2008 and 2009 (c)

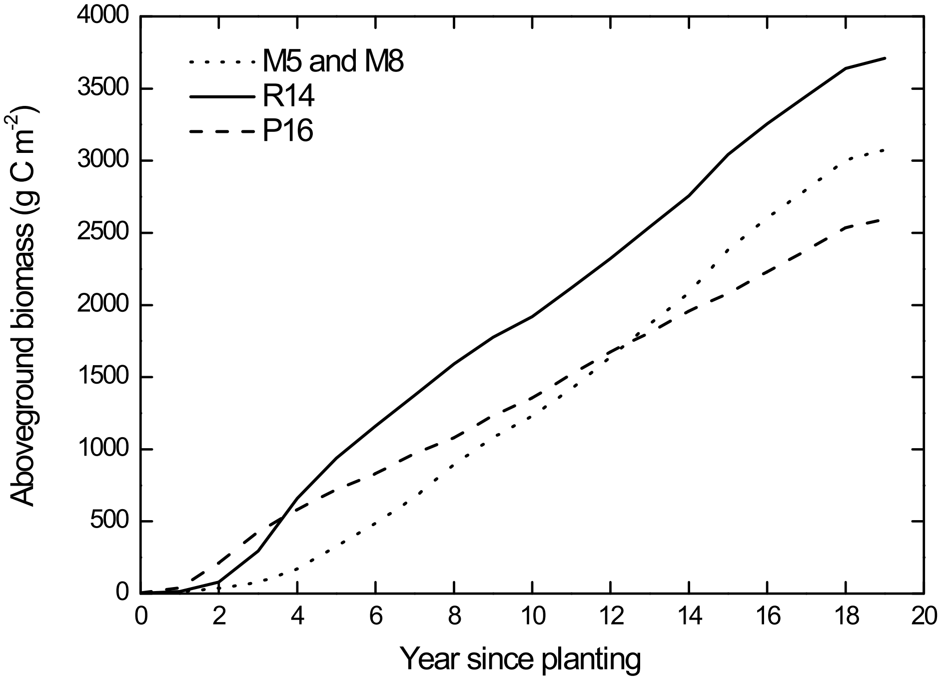

Figure 4 - 6. Modelled aboveground biomass C in the hybrid poplar plantations under different soil conditions over the first rotation

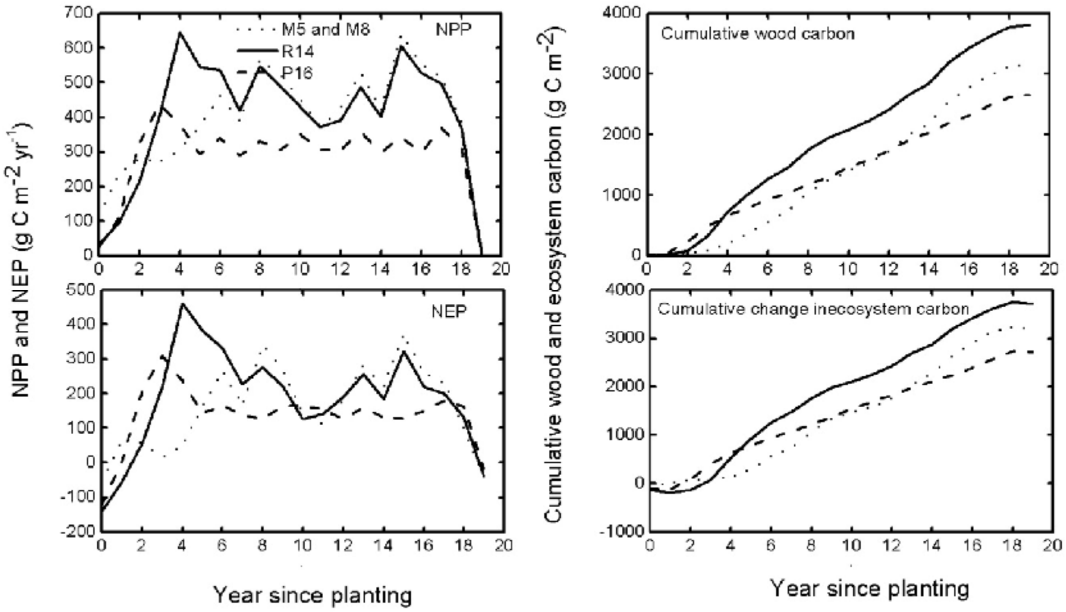

Figure 4 - 7. Modelled NPP, NEP, wood C and ecosystem C in the hybrid poplar plantations under different soil conditions over the first rotation

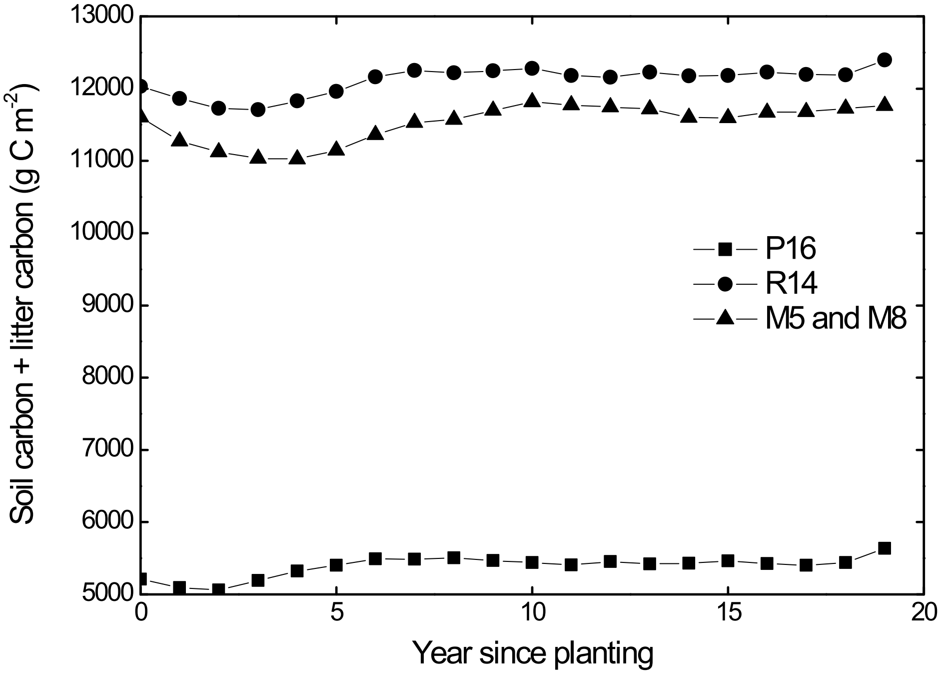

Figure 4 - 8. Soil and litter carbon dynamics over the first rotation in the four plantations

Chapter 5 Conclusions and synthesis

1. Conclusions

In this thesis research, the ecosystem processes of carbon cycling, e.g., soil respiration and net ecosystem exchange (represented by net ecosystem productivity, NEP), in response to land use changes (afforestation on previously agricultural lands) and stand development were studied using both experimental and modelling approaches. The major findings are as follows:

1. In a land use conversion trial (converting agricultural lands seeded with barley to a Walker poplar plantation in summer 2005, and another agricultural crop, where alfalfa was seeded from 2006 to 2008 for a barley-barley-alfalfa-alfalfa-alfalfa crop rotation), no afforestation effect was observed when soil respiration at the soil surface (including understory vegetation) was measured in 2007. However, significant afforestation effects on soil respiration were found in 2008 when photosynthetic activities of the understory vegetation were eliminated during soil respiration measurements. This indicates that the photosynthesis and respiration activities of the understory vegetation during the soil respiration measurement can mask the true rate of soil respiration.
2. Soil respiration and soil temperature at the 10 cm soil depth in both years and in both land uses had similar seasonal and diurnal variation. I found that soil temperature was the main control of soil respiration in the studied systems. The alfalfa plots released more CO_2 from the soil than the hybrid poplar plantation due to its higher soil respiration rate. The long-term temperature

sensitivity of soil respiration in the alfalfa plots was greater than that in the hybrid poplar plots. Therefore, under a future climate warming scenario, the soils seeded with alfalfa might be more sensitive to increased temperature and would release more CO_2.

3. Over the growing season in 2008, the agricultural ecosystem sequestered CO_2 (net ecosystem productivity: 0.9 Mg C ha^{-1}) from the atmosphere, while the hybrid poplar plantation lost CO_2 (net ecosystem productivity: -1.23 Mg C ha^{-1}), due to the low survival rate of the trees. This calculation, however, does not account for the understory vegetation growing in the hybrid poplar plots and if the contribution of the understory vegetation was accounted for, the system would likely be carbon neutral or negative as well.
4. In a chronosequence study of Walker poplar plantations (aged 4, 7, 13, and 15 years old in 2008), both soil respiration and net ecosystem productivity generally increased with stand age. Similar diurnal and seasonal variation in soil respiration were found in the different aged plantations, with inter-annual variation for each stand age in each of the three growing seasons from 2007 to 2009. Soil temperature explained most of the seasonal variation in 2008, a year with non-limiting soil water content. The 14-year-old plantation (age in 2009) had the greatest temperature sensitivity of soil respiration among the plantations in both 2008 and 2009. In 2009, heterotrophic respiration explained 66, 70 and 66% of the soil respiration in the 5-, 8-, and 14-year-old (age in 2009) plantations, respectively, with no significant stand age effect.

5. In the modelling study, modelled and measured soil respiration and aboveground biomass agreed well with each other. Plantations established on comparatively rich sites (higher contents of soil total nitrogen and good soil texture) accumulated the greatest amount of carbon over the first rotation (target rotation at 20 years), i.e., the 14-year-old plantation accumulated the greatest amount of carbon, followed by the 5 and 8-year-old plantations, and the 16-year-old plantation. Weeds had a significant effect on the early growth and survival of the trees. Modelled net ecosystem productivity (NEP), dominated by net primary productivity (NPP), increased with stand development and then decreased over the first rotation.

2. Synthesis

Afforestation of short-rotation, fast-growing hardwood species (such as hybrid poplars) on agricultural lands has been prevalent in Canada for supplying fibre over decades (Ward 2001) or as bio-energy feedstock production (Perlack et al. 2005). In terms of mitigating greenhouse gas emissions, these fast-growing plantation forests have been considered as an effective way to remove CO_2 from the atmosphere (FAO 2004) and thus to increase C storage in the soil. For example, the soils beneath some 12 to 16 year-old hybrid poplar plantations in north central United States accumulated 1.63 ±0.16 Mg C ha^{-1} yr^{-1} more soil carbon than adjacent agricultural soils (Hansen 1993). Most land use change (e.g., afforestation) studies have investigated long-term effects on soil carbon dynamics (Houghton 1999, Larionova et al. 2003, Laganiere et al. 2009), because it is nearly impossible to observe the difference in soil carbon content over the short term due to soil heterogeneity. However, other than the medium and long-term effects, in the context of monitoring greenhouse gas emissions, the short-term (especially the first few years after plantation establishment) effect of afforestation on carbon dynamics of newly established plantations should also be thoroughly investigated. The data indicate that, in the early years of an afforestation project, a net C loss is likely when the NPP of the planted trees is low and the site is frequently disturbed through cultivation to control weeds and other management practices. By comparing the hybrid poplar plots to the adjacent alfalfa plots, even though alfalfa could fix nitrogen, planting alfalfa would result in more CO_2 emissions from the soil. Furthermore, the greater long-term temperature sensitivity of soil respiration in the alfalfa plots indicated that soil carbon was less stable in this agricultural land use system. In addition, the non-significant difference in soil respiration between the two land uses when the underground vegetation, primarily weeds, was included in 2007 suggests that underground biomass should be evaluated as an important carbon pool in the initial years after afforestation. Even though the weeds were controlled, they re-grew very quickly and continued to affect the measurement of soil respiration. Since the typical rotation for agriculture in this area is planting barley for two years and then planting alfalfa for five to seven years, future research should continue to measure soil respiration over the whole rotation to see the difference between the two land uses. In the future, soil carbon content should be measured in the older plantations and adjacent agricultural lands to investigate the effect of afforestation on soil carbon dynamics.

After establishment of plantations, CO_2 fluxes from the soil and plantation ecosystem varied with stand development (Saiz et al. 2006, Grant et al. 2007b). Many factors are involved in the age effect on soil respiration and NEP which include the variation with stand age in litterfall, root biomass, microbial biomass, and water and nutrient availability (Grant et al. 2007a, Tang et al. 2009b). The data indicated that the stand age effect should be incorporated into empirical models when projecting soil respiration and NEP given the significant effect of stand age on these outputs. Readers should be cautioned that chronosequence studies of certain ecosystems require similar soil conditions, which is not the case in this study. In the current study, soil conditions such as soil texture, soil organic carbon and total nitrogen content varied among the different aged plantations, and the effect of stand age on soil respiration and NEP might be confounded by these factors. In future studies, plantations with similar soil conditions should be selected to investigate age effect when studying ecosystem processes. A few challenges were also identified when we were assessing the NEP, e.g., the possible error in the non-localised biomass equations for tree biomass calculations, and the trenching method used for determining R_h. When the trenching method was used to determine R_h, the value may have been over-estimated since the decomposition of the trenched roots also contributed to the R_h. Thus, in order to obtain an accurate R_h, it would be necessary to know the decomposition rate of the trenched roots in any future study, and remove this root decomposition from the measured "R_h". Future research should also focus on calibrating or developing site specific biomass equations for improving the accuracy of NPP calculations and improving the methods for determining R_h. In addition, understory biomass was not assessed in the current study which might contribute a significant component to the net ecosystem productivity, especially in young plantations with an open canopy (Netzer and Noste 1978).

The *ecosys* model was used to simulate soil respiration, NPP and NEP under different soil conditions. In the *ecosys* model, we planted the hybrid poplar with weeds seeded at a certain density and without any fertilizer, simulating the reality in an operational field. Overall, plantations would become C sinks from C source in 2 or 3 years after they were established based on the current modelling study. However, weeds at different densities and fertilization can be two critical factors impacting production of hybrid poplars (Welham et al. 2007). Therefore, in order to find the best plantation management for forest companies to maximize the production of these plantations in the current study, management controlling weeds (i.e., when and how to control the weeds) and the timing and quantity of fertilization should be simulated in the *ecosys* model. Based on the current study, weed effects on tree growth was quite significant in the first few years after establishment of the plantations, which might suggest that more than one-time cutting of weeds in the first few years would be required. In future modelling studies, weed densities in plantations with different soil conditions should be assessed in order to more accurately simulate the weed effect on tree growth. Some other variables, like leaf N: C ratio, P: C ratio, and weed biomass are suggested to be measured to compare with the model outputs to make sure that the ecosystem processes have been accurately simulated. Most importantly, when modelled and calculated NEP are compared with each other, instead of using calculated NEP (NEP = NPP- R_h), it is highly recommended that the NEP should be directly measured by eddy covariance considering the uncertainties inherent in the measured NPP and R_h values. Some other models, such as LINKAGES, or FORECAST, have also been used to project forest productivity under different forest managements (Pastor and Post 1985, Kimmins et al. 1999, Welham et al.

2007). Different from *ecosys* model, which projects forest productivity by simulating ecosystem processes, FORECAST or LINKAGES uses a hybrid simulation approach, combining empirical models on forest growth and then modifying them with a simulation of the temporal variation in competition for light and one or more nutrients, to predict the forest productivity. As a process model, *ecosys* simulates most of the important ecosystem processes, i.e., ecosystem-atmosphere energy exchange, canopy water relations, canopy C fixation, canopy respiration and senescence, nutrient uptake, plant growth and soil microbial activity, while in the hybrid ecosystem models, only a few ecosystem processes are simulated, for example light and nutrient competitions, which could limit the accuracy in predicting forest productivity (Kimmins et al. 1999).

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Appendix I: Characteristics of soils in the 0-10 cm layer at the studied sites.

Site	Bulk density (g cm^{-3})	Total C (g m^{-2})	Total N (g m^{-2})	Texture
Land use trial	0.78	7235±963a	629±70a	Loam
5-yr-old (M)	1.09	3274± 472b	292±35b	Silt loam
8-yr-old (M)	1.09	2814± 341b	256±36b	Silt loam
14-yr-old (R)	1.00	5282± 765c	419±64c	Loam
16-yr-old (P)	1.29	1925± 284d	178±27d	Sandy loam

Stand age in 2009; M: medium site; R: rich site; P: poor site; the lowercase letters with C and N values indicate the significance in mean difference between different site