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Soil respiration in four different land use systems in north central Alberta, Canada

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[1] This study compares soil respiration and its heterotrophic and autotrophic components in four land use types: agriculture, 2 and 9 year old hybrid poplar plantations, grassland, and a native aspen stand in north central Alberta, Canada, over a period of two growing seasons (2006 and 2007). The differences were examined with respect to substrate quality and quantity, fine root biomass, and nutrient availability, in addition to soil temperature and soil water content. Cumulative soil C loss via soil respiration averaged over the two growing seasons was (in decreasing order) 781, 551, 523, 502, and 428 g C m^{-2} for native aspen stand, 9 year old hybrid poplar plantation, grassland, agriculture and 2 year old hybrid poplar plantation, respectively. We found that ~75% of soil respiration in the native aspen stand originated from the top 7.5–10 cm litter-fibric-humus layer. Seasonal heterotrophic and autotrophic respiration among the land uses ranged from 97 to 272 and 333 to 560 g C m^{-2}, respectively, contributing up to 35% and 83% of total soil respiration, respectively. The variability in soil respiration across different land uses was explained mainly by site differences in soil temperature (88–94%). Soil respiration followed a pronounced seasonal trend: increasing during the growing season and converging to a minimum in the fall. Soil respiration under different land uses was influenced by (1) ecosystem C stock, (2) temperature sensitivity (Q_{10}) of organic matter present, and (3) organic matter decomposability as indicated by the natural abundance of δ^{13}C. Heterotrophic respiration was influenced by soil temperature, while autotrophic respiration was influenced by fine root biomass and nutrient (NO_3^- and P) availability. These results are useful in estimating potential responses of soil respiration and its components to future land management and climate change.

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1. Introduction

[2] Concerns over increasing atmospheric carbon dioxide (CO_2) concentrations and its likely effects on the global climate prompted extensive research on all aspects of the global carbon (C) cycle. Soils play an important role in the global C cycle because they both store and release large quantities of C to the atmosphere through soil respiration (R_s). In addition to fire, R_s is the primary pathway through which C fixed through photosynthesis returns to the atmosphere [*Raich et al.*, 2002]. Soil respiration can account for up to 90% of total ecosystem respiration [*Hanson et al.*, 2000] and is therefore one of the major components to consider in understanding ecosystem-atmosphere C exchange. There is considerable interest in the effects of land use change on soil C fluxes and storage [*Guo and Gifford*, 2002; *Hibbard et al.*, 2005; *Post and Kwon*, 2000] specifically on R_s [e.g., *Ellert and Janzen*, 1999; *Franzluebbers*, 2005]. *Houghton* [1999] estimated that globally land use change caused approximately 123 Pg C to be released to the atmosphere between 1850 and 1990, with the most important land use change being the expansion of agriculture, with croplands, forests-pasture and shifting cultivation accounting for 68, 13, and 4%, respectively, of the net ecosystem C loss to the atmosphere.

[3] The production of CO_2 in the soil is primarily due to autotrophic respiration by roots and rhizospheric organisms (R_a) and heterotrophic respiration (R_h) by microbes decomposing detritus, root exudates, and organic matter [*Hanson et al.*, 2000]. The R_h ultimately controls soil C storage while R_a reflects plant activity and the allocation of organic compounds to root biomass from aboveground [*Binkley et al.*, 2006]. Partitioning R_s to R_h and R_a is therefore impor-

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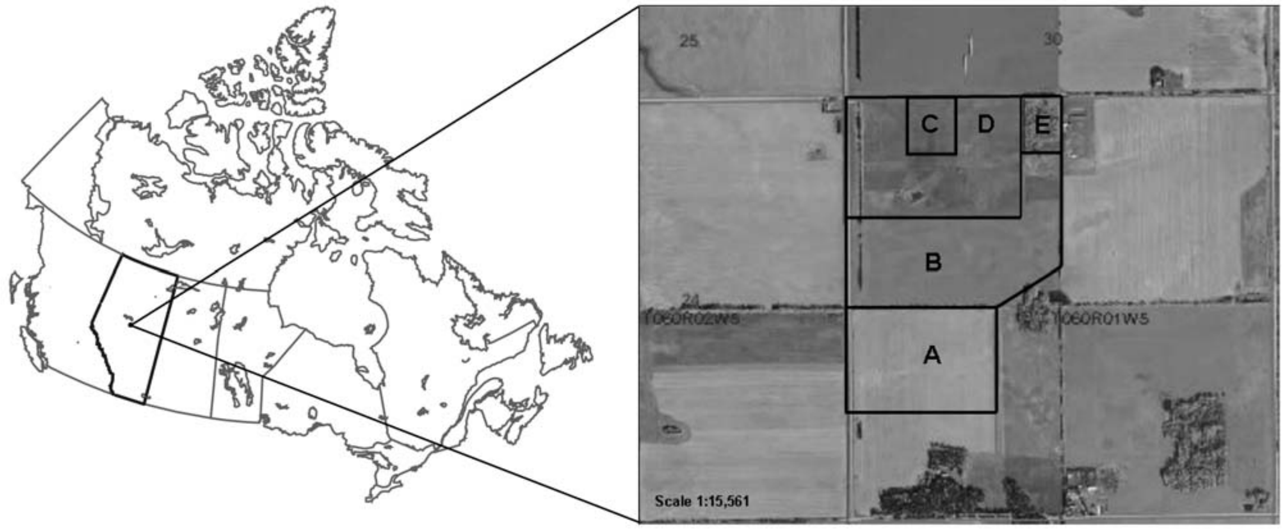

Figure 1. Location of land use study sites (location A, agriculture; location B, 2 year old hybrid poplar plantation; location C, 9 year old hybrid poplar plantation; location D, grassland; location E, native aspen stand) in Linaria, Alberta, Canada (54°12′ N, 114°8′ W). The source of the aerial photo is http://www.agriculture.alberta.ca. The use of the aerial photo by the authors is done without any affiliation with or endorsement by the Government of Alberta. Reliance upon the authors' use of these materials is at the risk of the end user.

tant in understanding C cycling because R_h and R_a may respond differently to environmental controls, implying different behaviors at different timescales and for different plant communities. Recent reviews by *Hanson et al.* [2000], *Bond-Lamberty et al.* [2004], and *Subke et al.* [2006] have indicated that R_a generally accounts for 50% of R_s across a range of ecosystems and timescales. *Hanson et al.* [2000], based on results in 50 publications, reported mean R_a contributions of 48 and 37% in forest and nonforest ecosystems, respectively. In addition, the contribution of R_a has large seasonality, usually low during the dormant season and high during the active growing season [*Hanson et al.*, 2000]. The dynamics of the two components, R_a and R_h, is controlled by several abiotic and biotic factors including soil temperature [*Rustad et al.*, 2001], soil water content [*Liu et al.*, 2002], soil drainage [*Freeman et al.*, 1993], soil fertility [*Butnor et al.*, 2003], availability of C substrates for microorganisms [*Seto and Yanagiya*, 1983], plant root densities and activities [*Maier and Kress*, 2000], plant photosynthetic activity [*Bhupinderpal-Singh et al.*, 2003], and soil organism population size [*Rai and Srivastava*, 1981]. All of these variables are influenced by land use or land cover type [*Raich and Tufekcioglu*, 2000].

[4] Understanding the factors that affect R_s is essential to assess the impacts of land use change and predict outcomes under future land use scenarios. Although there have been many studies on R_s, there have been few studies that quantified the effects of land use change, i.e., vegetation change on a specific site. We studied R_s in four adjacent ecosystems: native aspen forest, 2 and 9 year old hybrid poplar plantations, grassland, and agriculture. The objectives of this study were: (1) to measure the seasonal and diurnal changes in R_s under different land uses, (2) to partition R_s into R_h and R_a, and (3) to examine the factors affecting variations in R_s, R_h, and R_a under different land uses.

2. Methods

2.1. Site Description

[5] The study sites are located near Linaria (54°12′ N, 114°8′ W), approximately 25 km west of Westlock, in north central Alberta, Canada (Figure 1). The study area has a continental climate, with cold winters and warm summers which provide an approximate growing season of 180–185 days between the months of May and November [*Alberta Agriculture, Food, and Rural Development* (*AAFRD*), 2003]. Climate normals for the study area, based on 12 years of data collected at nearby Westlock weather station (Environment Canada, Canadian climate data online 1993–2007, http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html, 2005) show that the area has a mean annual temperature of 3°C and mean annual precipitation of 463 mm (350 mm of which falls as rain and 113 mm as water equivalent of snow). The soil is classified as a Dark Gray Luvisol in the Canadian system of soil classification on medium textured till characterized by poor drainage, and undulating, low relief landform with a slope of 2%.

[6] Three experimental plots (20×20 m^2) were set up in four different land use systems in this study: (1) an agricultural field used for grains and canola production following a 4 year rotation of barley (*Hordeum vulgare* L.) – barley – wheat (*Triticum aestivum* L.) – canola (*Brassica napus* L.), (2) 2 and 9 year old hybrid poplar (*Populus deltoides* x *Populus x petrowskyana* cv. Walker) plantations (three plots in each plantation age), (3) a grassland seeded with a mixture of *Festuca arundinacea* Schreb. (tall fescue), *Dactylis glomerata* L. (orchard grass), and *Trifolium pratense* L. (red clover), and (4) a native forest stand of

trembling aspen (*Populus tremuloides* Michx.). Detailed description of the four different land use sites (including soil physical and chemical properties) are given by *Arevalo et al.* [2009].

2.2. Measurement of Soil CO_2 Concentrations and Diffusivity

[7] Soil CO_2 concentrations were continuously measured at two depths every 2 h, from 22 May 2007 to 19 November 2007, using Vaisala CARBOCAP solid-state infrared CO_2 sensors (Models GMM221 and GMM222; Vaisala Oyj, Helsinki, Finland). At the center of one 20 m × 20 m plot in each of the study sites, one GMM222 probe (measurement range of 0–10000 μmol CO_2 mol^{-1}) was installed horizontally at 2 cm depth while a GMM221 (range of 0–20000 μmol CO_2 mol^{-1}) was installed vertically at 20 cm depth. The sensors were separated horizontally by 5 cm. Data loggers (Model CR-10X, Campbell Scientific Inc., Logan, UT, USA) were used to record CO_2 concentration measurements. The systems were powered by two 12 V batteries connected in series, charged by photovoltaic panels (5–15 Watts).

[8] To determine soil CO_2 diffusivity on each of the study sites, undisturbed soil cores (11 cm inside diameter, 10 cm height) were sampled at 0–10 and 10–20 cm soil depths in the vicinity of the collars and Vaisala probes. Diffusivity in these soil cores was measured at different soil water content values. Measurements were made, under steady state conditions using CO_2 as the diffusing gas, in the Soil Physics laboratory at the University of British Columbia, using the technique described by *Jassal et al.* [2005].

2.3. Chamber Measurement of R_s and R_h

[9] To validate R_s calculated using soil CO_2 concentrations and diffusivity measurements, chamber measurements were made with a LI-COR 6400 portable photosynthesis system equipped with a LI-COR 6400–09 portable opaque soil chamber attachment (LI-COR Biosciences Inc., Lincoln, NE, USA). These measurements were made at 15 to 27 locations in each land use site using collars made from polyvinyl chloride (PVC) pipe (10 cm inside diameter and 6 cm long), beveled on one end to reduce soil compaction and disturbance during insertion into the soil. These collars were gently hammered approximately 2 cm into the soil, leaving about 4 cm above the soil surface and were left in place for the duration of the study.

[10] As trees in the hybrid poplar plantations were planted operationally on a square spacing and such configuration is known to cause spatial variation in soil respiration [*Saurette et al.*, 2006], a stratified random sampling design for the locations of the soil collars (distance from trees) was used to account for the spatial variability in soil properties and respiration rates. An equal number of collars were placed close to the base of a tree, midway between two trees, and at the center of the square formed by four trees in each plot. Each spatial arrangement of collars was replicated three times, which resulted to nine collars per plot or 27 collars per site. Collars at the agriculture, grassland, and native aspen sites were installed using a random sampling design using five collars per plot (or 15 collars per site). The R_s measurements on all the collars were made every four weeks during the growing seasons of 2006 (28 June, 27 July, 24 August, and 26 September) and 2007 (29 May, 28 June, 26 July, and 30 August). All R_s measurements were carried out between 1000 and 1600 h (local summer time).

[11] To determine the contribution of R_h to R_s, a modified root exclusion trenched plot technique was used following *Kelting et al.* [1998]. This relied on severing all the roots around the perimeter of PVC collars in order to eliminate root respiration. For this purpose, nine PVC collars (10 cm inside diameter and 32.5 cm long) per study site were inserted (on 17 May 2006) 30 cm into the soil. In order to avoid plant activity, vegetation within the collars was regularly removed by clipping. Measurements of R_s (from the short collars) and R_h (from the long collars) were made at four-week intervals (28 June, 27 July, 24 August, and 26 September 2006). The contribution of R_a was then determined by subtracting R_h from R_s.

2.4. Soil Temperature and Moisture Measurements

[12] Soil temperature (T_s) and soil volumetric water content (θ_v) were continuously measured from 30 May 2006 to 19 November 2007 using HOBO U12 temperature sensors (Model TMC6-HD, Onset Computer Corp., Bourne, MA, USA) and porous matrix tensiometers (Watermark Sensor type WMSM, Delta-T Devices Ltd., Cambridge, UK), respectively. These sensors were also installed at the 2 and 20 cm depths but approximately 30 cm away from the Vaisala CO_2 sensors. The temperature and water content sensors were connected to a HOBO U12 external data logger (Model U12–006, Onset Computer Corp., Bourne, MA, USA) programmed to take readings every 2 h when CO_2 concentrations were measured by the Vaisala sensors.

[13] Soil temperature and soil volumetric water content were also measured manually at the 0–6 cm depth near (within 20–30 cm) each PVC collar. Soil temperature was measured using a soil temperature probe (LI-COR 6000–09TC, LI-COR Biosciences Inc., Lincoln, NE, USA), while θ_v was measured with a portable soil-water frequency domain reflectometry sensor (ThetaProbe ML2-X, Delta-T Devices, Cambridge, UK).

2.5. Calculation of Soil Respiration Rates

[14] Using measured soil CO_2 concentrations at the 2 and 20 cm depths and ambient atmospheric CO_2 concentration at the soil surface (zero depth), we calculated CO_2 flux in the soil at the 1 and 11 cm depths (midpoints of 0–2 cm and 2–20 cm layers) using Fick's law of diffusion:

$$F_i = -D\frac{\partial C}{\partial z} \tag{1}$$

where F_i is the soil CO_2 flux (μmol m^{-2} s^{-1}) at depth i (m), D_i is the diffusivity of CO_2 in the soil (m^2 s^{-1}) at depth i, and $\partial C/\partial z$ is the vertical soil CO_2 concentration gradient (μmol m^{-4}). Linear gradients were assumed between the 0 and 2 cm depths and between the 2 and 20 cm depths separately, based on the shape of soil CO_2 profiles with concentration measurements at discrete soil depths reported in the literature [e.g., *Drewitt et al.*, 2005; *Jassal et al.*, 2005]. Our periodic chamber measurements indicated that ambient CO_2 concentrations at the soil surface generally varied between 380 and 425 ppm, except in the native aspen stand where they were somewhat higher. The F_1 was assumed to represent the total CO_2 efflux originating at the soil surface and is referred to hereafter as R_s; F_{11} represents the efflux originating from below the 11 cm depth, referred to as R_{sub}. As the native aspen stand had about 7.5–10 cm LFH (litter-fibric-humus) layer, R_s was also measured in the native aspen stand after removing the LFH layer and is referred to as $R_{NAT\text{-}LFH}$.

[15] Diffusivities of CO_2 in the soil were computed using the equation:

$$D_s = \xi D_a \tag{2}$$

where ξ is the gas tortuosity factor and D_a is the molecular diffusivity of CO_2 in air. D_a was corrected for variations in temperature and barometric pressure using the equation:

$$D_a = D_{a0}\left(\frac{T_a}{293.15}\right)^{1.75}\left(\frac{101.3}{P}\right) \tag{3}$$

where T_a is the air temperature in K, P is the air pressure in kPa, D_{a0} is the CO_2 diffusivity in air at 293.15 K and 101.3 kPa, which is given as 14.7 $mm^2\ s^{-1}$ [*Jones*, 1992]. The tortuosity factor, ξ, obtained using measured values of D_s and ε was found to be independent of soil depth and soil matrix, and was parameterized with air-filled porosity using a nonlinear relationship [*Curie*, 1965],

$$\xi = n\varepsilon^m \tag{4}$$

where ε is the soil air-filled porosity and the n and m are coefficients determined empirically from the undisturbed soil cores. Air-filled porosity was calculated based on its relationship with soil bulk density (ρ_b), particle density (ρ_m), total soil porosity (φ), and volumetric water content (θ_v):

$$\varepsilon = \phi - \theta_v = 1 - \frac{\rho_b}{\rho_m} - \theta_v \tag{5}$$

[16] In order to parameterize R_s, regression analyses were performed on R_s (obtained by the LICOR 6400–09) and T_s or θ_v measurements. Exponential relationships between R_s and T_s were found to be the best fit:

$$R_s = a\exp^{bT_s} \tag{6}$$

where R_s is the soil surface respiration at soil temperature T_s, coefficient a is the soil respiration rate at temperature zero (i.e., basal rate), and coefficient b is the sensitivity of R_s to T_s. The regression coefficients a and b determined for each land use were used to estimate continuous 2-hourly values of R_s, which were then used to compute daily and seasonal R_s for each study site and year.

[17] In order to determine temperature sensitivity of soil from each of the land uses, the same exponential relationship was fit and the b values in equation (6) were used to calculate Q_{10}:

$$Q_{10} = \exp^{10b} \tag{7}$$

where Q_{10} is the relative increase in R_s for every 10°C increase in T_s. Mean values of Q_{10} were determined for each land use site using data from the two study years.

2.6. Statistical Analyses

[18] Cumulative soil CO_2 efflux through R_s for each growing season (1 June to 30 September for 2006 and 2007) for each land use type was calculated by adding all the daily R_s values. Uncertainty associated with cumulative soil CO_2 efflux through R_s and its components were estimated by assigning a random (measurement) error of 20% to each daily value. The daily fluxes with the ±20% variation were resampled using bootstrap Monte Carlo method and seasonal sums calculated. This procedure was repeated 500 times and uncertainty was determined at 95% confidence level. Temporal variations in R_h, R_a, and the contribution of R_h to R_s (i.e., R_h/R_s), both among different land use types and from month to month, were analyzed using analysis of variance (ANOVA) with repeated measures coupled with Tukey's Studentized Range Test in SAS [*SAS Institute Inc.*, 2004]. Interaction effects were elucidated using the *pdiff* option in SAS. To determine correlations of R_h and R_a and soil biophysical variables (pH, soil organic N and C, particulate organic matter, NH_4^+, NO_3^-, available P, microbial biomass C and N, and fine root biomass) that were simultaneously measured as part of a larger study [see *Arevalo et al.*, 2009], Pearson product-moment correlations were carried out in SAS. Significance was tested using α value = 0.05, except for Pearson correlations where two levels of significance were recognized: weakly significant (α value = 0.10) and significant (α value = 0.05).

3. Results

3.1. Weather

[19] Year 1 (1 June to 30 September 2006) was slightly warmer with the seasonal mean T_a of 15.5°C compared to 14.6°C in Year 2 (1 June to 30 September 2007, Figure 2); and compared to the long-term (1994–2006) seasonal mean (15.0°C) for the area (Environment Canada, Canadian climate data online 1993–2007, http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html, 2005). Year 1 was also slightly wetter with a total of 271 mm rainfall during the four months summer period, compared to 226 mm during the same period in Year 2, although both were within the normal seasonal range of 158–415 mm recorded for the area.

[20] Mean daily soil temperature at the 2 and 20 cm depths followed similar seasonal trends at all land use sites (Figure 2), with T_s in the range 4–39°C, peaking in mid-July. These temperatures were consistently somewhat cooler at the 9 year old hybrid poplar plantation and native aspen stand compared to the agriculture, 2 year old hybrid poplar and grassland sites. Soil water content was highest in early June, as a result of snowmelt, and remained in the range 0.13–0.45 $m^3\ m^{-3}$ throughout both growing seasons. Soil moisture status at all land use sites was within optimum conditions (field capacity = 0.40–0.50 $m^3\ m^{-3}$, permanent wilting point = 0.13–0.17 $m^3\ m^{-3}$).

3.2. Chamber- and Gradient-Measured Soil Respiration

[21] A comparison of chamber-measured R_s values with those calculated using soil CO_2 concentration gradients and diffusivities (equations (1) and (2)) showed that the two agreed very well (slope 1.008, r^2 = 0.96, Figure 3). Fitting

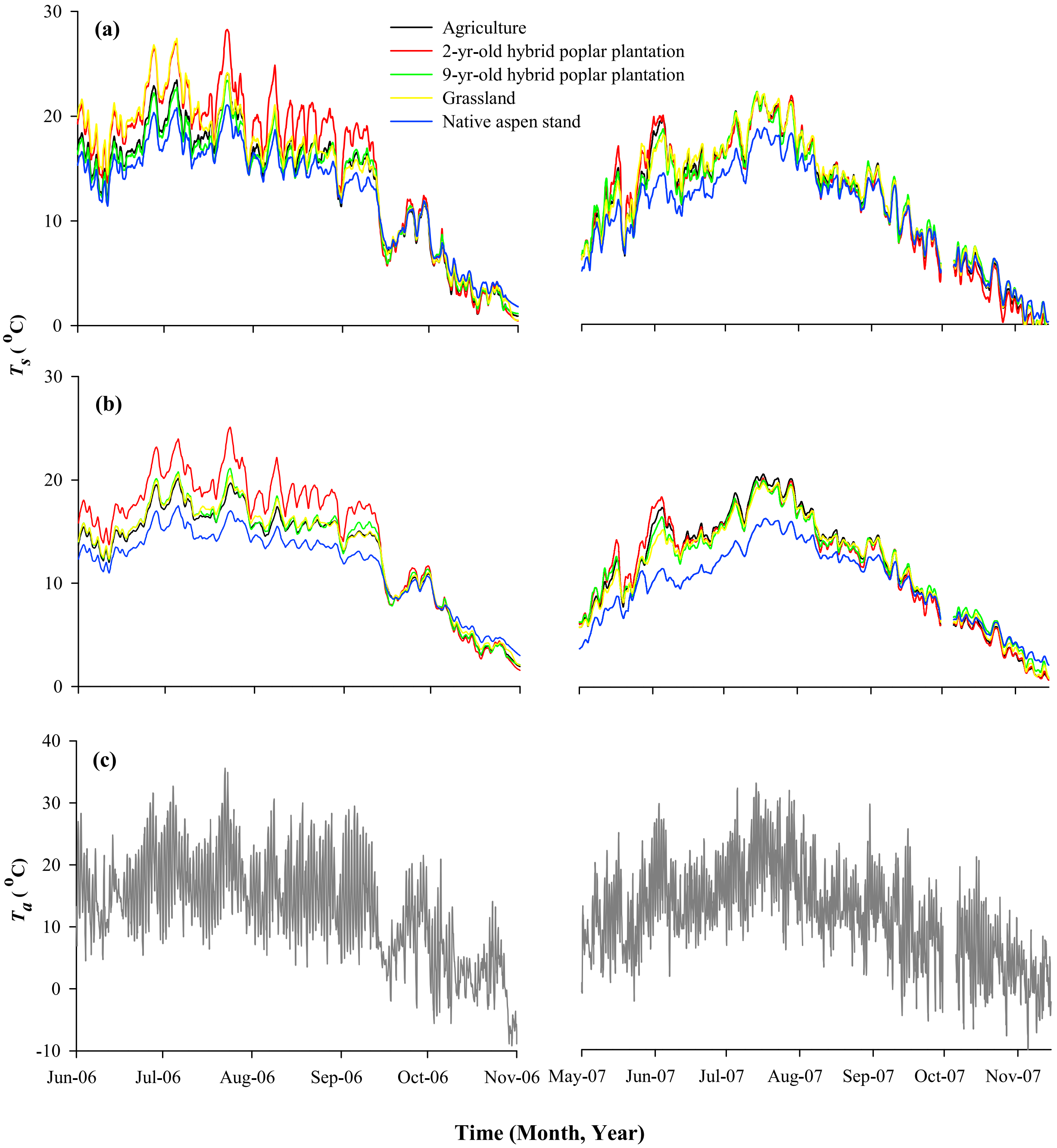

Figure 2. Seasonal patterns of soil temperature (T_s) at (a) 2 cm and (b) 20 cm depths in various land uses; and (c) air temperature (T_a) during the 2 year study period in Linaria, Alberta.

equation (6) to chamber-measured R_s values from Year 1 and Year 2 showed that T_s (range: −2.5 to 27.0°C) explained 88–94% of the variation in R_s (Table 1). On the other hand, θ_v predicted R_s poorly ($r^2 = 0.12–0.42$, data not shown). The calculated Q_{10} values differed among land use types in the order of grassland (1.88) < native aspen stand (1.93) < 9 year old hybrid poplar plantation (2.11) < 2 year old hybrid poplar plantation (2.21) < agriculture (2.70).

3.3. Seasonal Soil Respiration Under Different Land Uses

[22] The R_s ranged from a minimum of 0.12 to 0.24 μmol CO$_2$ m^{-2} s^{-1} to a maximum of 6.2 to 11.6 μmol CO$_2$ m^{-2} s^{-1} depending on land use and time of year (Figure 4). During both years, temporal variation in R_s corresponded closely to seasonal changes in T_s for all land uses (Figures 2 and 4), reaching maximum rates between mid-June and mid-July when soil temperatures were highest. The lowest rates were observed in late fall. Chamber measurements made at 15–27 collars within each land use indicated lesser spatial variability in the 2 year old hybrid poplar plantation, grassland, and agriculture (SD of 0.35, 0.38, and 0.59 μmol CO$_2$ m^{-2} s^{-1}, respectively) than in the 9 year old hybrid poplar plantation and native aspen stand (SD of 0.69 and 0.97 μmol CO$_2$ m^{-2} s^{-1}, respectively).

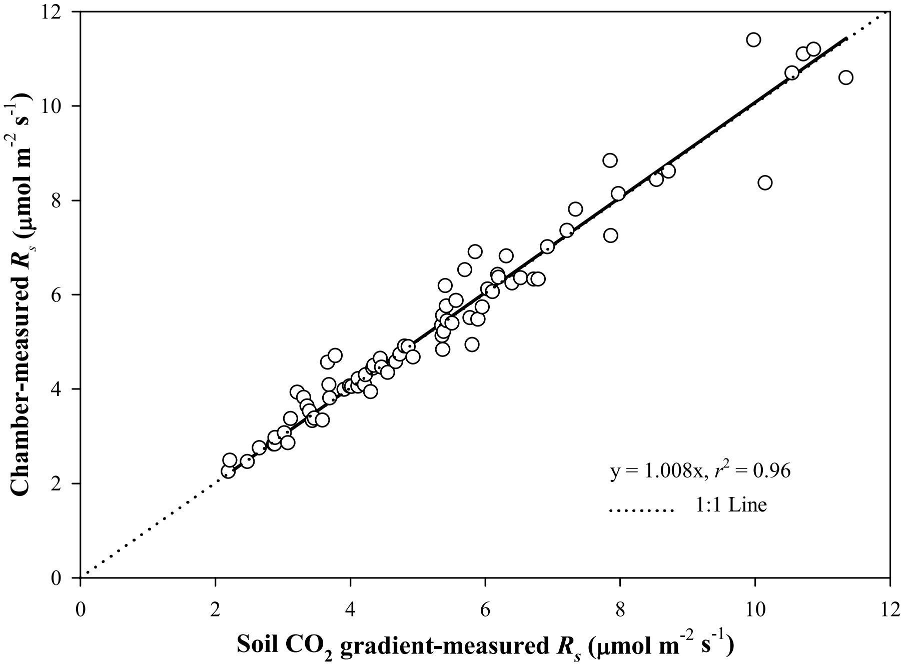

Figure 3. Comparison of soil CO_2 effluxes (R_s) measured using the chamber and the soil CO_2 gradient techniques.

[23] Cumulative seasonal (1 June to 30 September) soil C efflux due to R_s was generally higher in Year 1 than in Year 2 for all land uses (Table 2). Averaged across the two growing seasons, R_s was highest in the native aspen stand (781 g C m^{-2}) of which approximately 75% (586 g C m^{-2}) originated from the LFH layer and the balance from the mineral soil ($R_{NAT\text{-}LFH}$ = 194 g C m^{-2}). Other land uses released smaller amounts of C, which, averaged over the two growing seasons, ranked in the order: 9 year old hybrid poplar plantation (551 g C m^{-2}) > grassland (523 g C m^{-2}) > agriculture (502 g C m^{-2}) > 2 year old hybrid poplar plantation (428 g C m^{-2}). The seasonal soil CO_2 efflux originating from R_{sub}, varied from a minimum of 136 g C m^{-2} in the native aspen stand, followed by 2 year old hybrid poplar plantation (210 g C m^{-2}), 9 year old hybrid poplar plantation (216 g C m^{-2}), grassland (243 g C m^{-2}), to a maximum of 358 g C m^{-2} in the agricultural field. We found that R_s was highly related to aboveground biomass C (r = 0.66, p value = 0.008), belowground biomass C (r = 0.77, p value = 0.001), total ecosystem biomass C (r = 0.80, p value = <0.001), and marginally related to soil C (r = 0.54, p value = 0.036).

3.4. Diurnal Variation in Soil Respiration Under Different Land Uses

[24] Like seasonal variations in R_s, the 2-hourly measurements of R_s corresponded closely to diurnal temperature variations (Figure 5). The R_s originating from the mineral soil (excluding the LFH layer in the native aspen stand) increased after 0800 h and peaked at around 1500–1700 h for all land uses during the early, middle, and late parts of the growing season, typically lagging T_s by 1–2 h. Diurnal variations in θ_v (at both measurement depths) did not change much over the growing season and showed no effect on diurnal variation in R_s. Mean daily R_s across different land uses were 3.9, 6.2, and 2.8 μmol CO_2 m^{-2} s^{-1} during the early, middle, and late parts of the growing season, respectively. In the middle of the growing season, the 9 year old hybrid poplar plantation had the highest R_s (10.0 μmol CO_2 m^{-2} s^{-1}) followed by grassland (6.9 μmol CO_2 m^{-2} s^{-1}), agriculture (6.6 μmol CO_2 m^{-2} s^{-1}), 2 year old hybrid poplar plantation (4.0 μmol CO_2 m^{-2} s^{-1}), and native aspen stand (2.0 μmol CO_2 m^{-2} s^{-1}).

Table 1. Analysis of the Dependence of Measured Soil Surface Respiration, R_s, on Soil Temperature, T_s[a]

	R_s (μmol CO_2 m^{-2} s^{-1})		T_s (°C)					
Land Use	Minimum	Maximum	Minimum	Maximum	a	b	r^2	Q_{10}
Agriculture	0.1	11.6	−0.4	19.3	0.80	0.10	0.89	2.70
2 year old hybrid poplar	0.2	6.2	−2.2	21.6	0.93	0.08	0.94	2.21
9 year old hybrid poplar	0.1	9.9	−2.5	24.2	1.29	0.07	0.89	2.11
Grassland	0.2	7.3	−1.6	27.0	1.53	0.06	0.93	1.88
Native aspen stand	0.2	9.5	−0.7	25.8	2.24	0.07	0.88	1.93

[a] Using the equation $R_s = a \exp^{bT_s}$; and Q_{10} (unitless, temperature sensitivity parameter, relative change in R_s for a 10°C change in T_s) across various land uses in Linaria, Alberta.

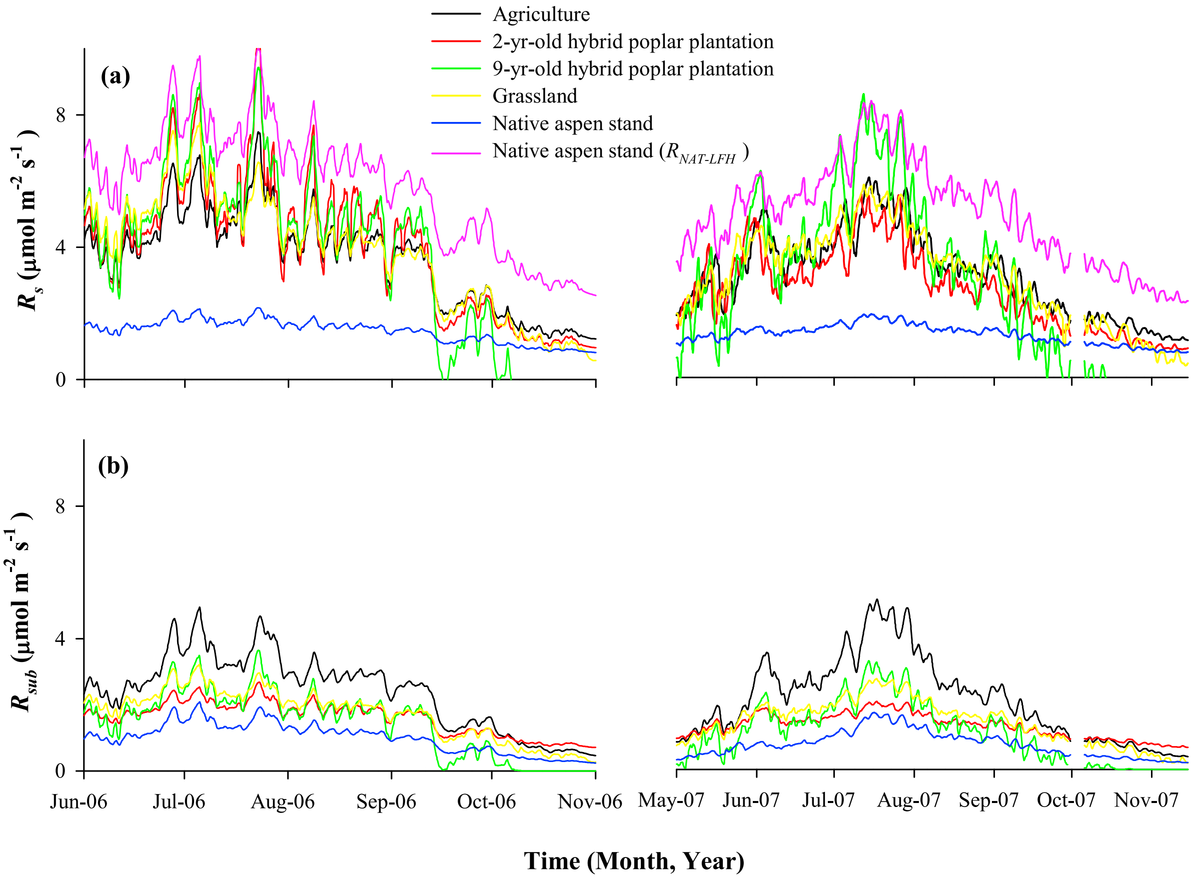

Figure 4. Seasonal patterns of soil respiration at (a) the soil surface (R_s) and at (b) 11 cm depth (R_{sub}) in various land uses; and at LFH layer in the native aspen stand ($R_{NAT-LFH}$) during the 2 year study period in Linaria, Alberta.

3.5. Heterotrophic and Autotrophic Respiration

[25] Cumulative C released due to R_h (decomposition) was highest in the native aspen stand followed by agriculture > 9 year old hybrid poplar plantation > 2 year old hybrid poplar plantation > grassland whereas cumulative C released in R_a (autotrophic respiration) was highest in the native aspen stand followed by the grassland > 9 year old hybrid poplar plantation > agriculture > 2 year old hybrid poplar plantation (Table 2). Mean R_h/R_s, across all sampling dates, was found to be highest at the agriculture and native aspen sites (R_h/R_s = 0.35 and 0.33, respectively), intermediate at the 2 and 9 year old hybrid poplar plantation sites (R_h/R_s = 0.26 and 0.25, respectively), and lowest at the grassland site (R_h/R_s = 0.17). The average contribution of R_h to R_s (R_h/R_s) for all land uses over the growing period was 0.27.

[26] Mean monthly R_h was not much different between native aspen and agriculture (1.92 and 1.89 μmol CO$_2$ m^{-2} s^{-1}, respectively, Figure 6) but was higher than in the 9 year old hybrid poplar plantation, grassland, and 2 year old hybrid poplar plantation (1.22, 0.96, and 0.86 μmol CO$_2$ m^{-2} s^{-1}, respectively). Within each land use, R_h was significantly different between sampling dates (agriculture: p value = < 0.001, 2 year old hybrid poplar plantation: p value = 0.001, 9 year old hybrid poplar plantation: p value = < 0.001, grassland: p value = 0.003, and native aspen stand: p value = <0.001). The general pattern for all land uses showed R_h to be higher only in June, although at the native aspen stand R_h was found to increase from 1.95 μmol CO$_2$ m^{-2} s^{-1} in June to 3.00 μmol CO$_2$ m^{-2} s^{-1} in July and then decline to a stable rate of 1.36 μmol CO$_2$

Table 2. Cumulative Seasonal Soil C Efflux From 1 June to 30 September[a]

	Components of Soil Respiration (g C m^{-2})				
Land Use	R_s	R_{sub}	R_h	R_h/R_s	R_a
		2006			
Agriculture	530 ± 26	359 ± 24	186 ± 35	0.35	344 ± 65
2 year old hybrid poplar	449 ± 20	228 ± 14	116 ± 22	0.26	333 ± 63
9 year old hybrid poplar	598 ± 33	232 ± 23	148 ± 22	0.25	450 ± 68
Grassland	569 ± 32	257 ± 11	97 ± 10	0.17	473 ± 47
Native aspen stand	833 ± 41	149 ± 25	272 ± 44	0.33	560 ± 90
$R_{NAT-LFH}$	203 ± 32				
		2007			
Agriculture	474 ± 22	357 ± 27		n.d.	
2 year old hybrid poplar	408 ± 19	192 ± 35		n.d.	
9 year old hybrid poplar	504 ± 28	201 ± 34		n.d.	
Grassland	478 ± 22	229 ± 20		n.d.	
Native aspen stand	728 ± 38	123 ± 28		n.d.	
$R_{NAT-LFH}$	185 ± 42				

[a] From the soil surface (R_s) and subsurface (R_{sub}) over 2 study years and the corresponding proportions originating from heterotrophic (R_h and R_h/R_s) and autotrophic (R_a) respirations in the first study year from various land uses in Linaria, Alberta. Values are cumulative estimates ± uncertainty at 95% confidence. $R_{NAT-LFH}$, respiration originating from the mineral soil under the forest floor in the NAT stand; n.d., not determined.

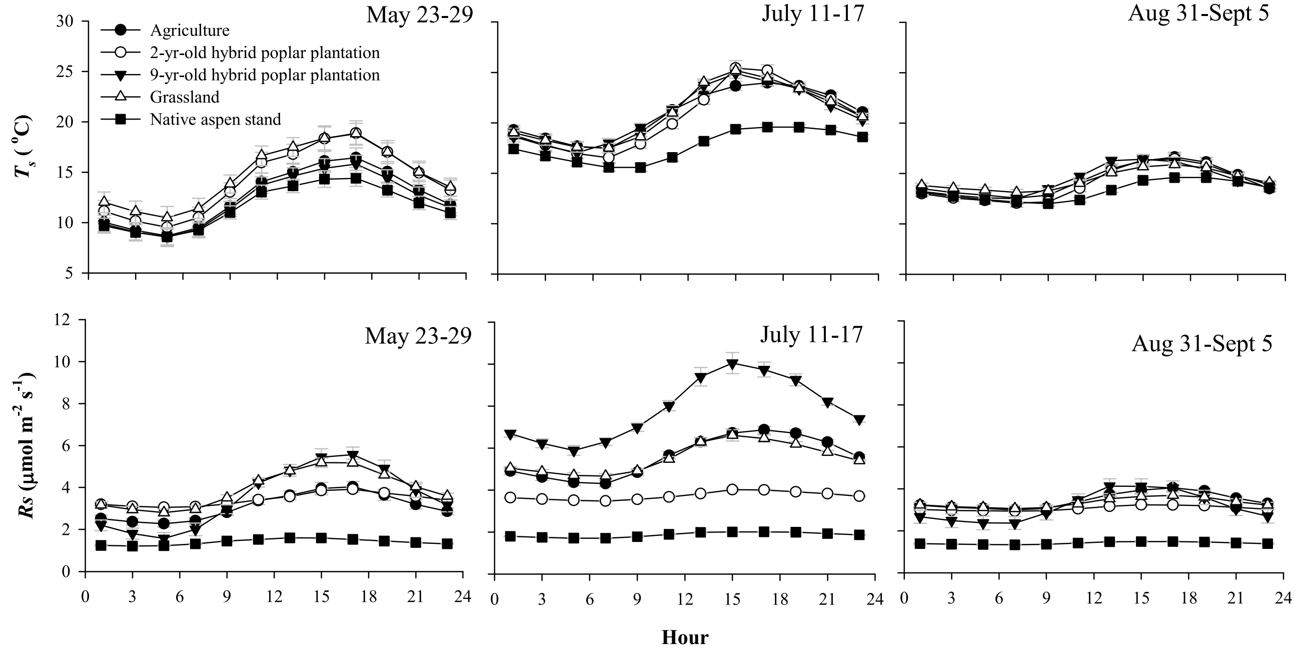

Figure 5. Mean diurnal patterns and their standard errors of soil temperature at the 2 cm depth and soil respiration during the early (23–29 May), middle (11–17 July), and late (31 August to 5 September) parts of the growing season of 2007 across various land uses in Linaria, Alberta.

m^{-2} s^{-1} for the remainder of the study period. R_h was positively correlated with T_s ($r = 0.79$, p value = 0.100).

[27] At the agricultural site, R_a did not differ appreciably among the four sampling dates (p value = 0.997) and hence appeared stable throughout the growing season whereas at the other land use sites, R_a varied significantly between sampling dates (2 year old hybrid poplar plantation: p value = <0.001, 9 year old hybrid poplar plantation: p value = <0.001, grassland: p value = <0.001, native aspen stand: p value = <0.001). At the 2 and 9 year old hybrid poplar plantations and grassland sites, R_a was highest in July and lowest in September, whereas at native aspen site, R_a was statistically similar in June, July, and August (averaging 6.31 μmol CO$_2$ m^{-2} s^{-1}) but decreased significantly during September to 1.65 μmol CO$_2$ m^{-2} s^{-1} (p value = <0.001). Averaged over all four sampling dates, R_a was significantly higher for the native aspen stand, grassland and 9 year old hybrid poplar sites (4.50, 4.36,

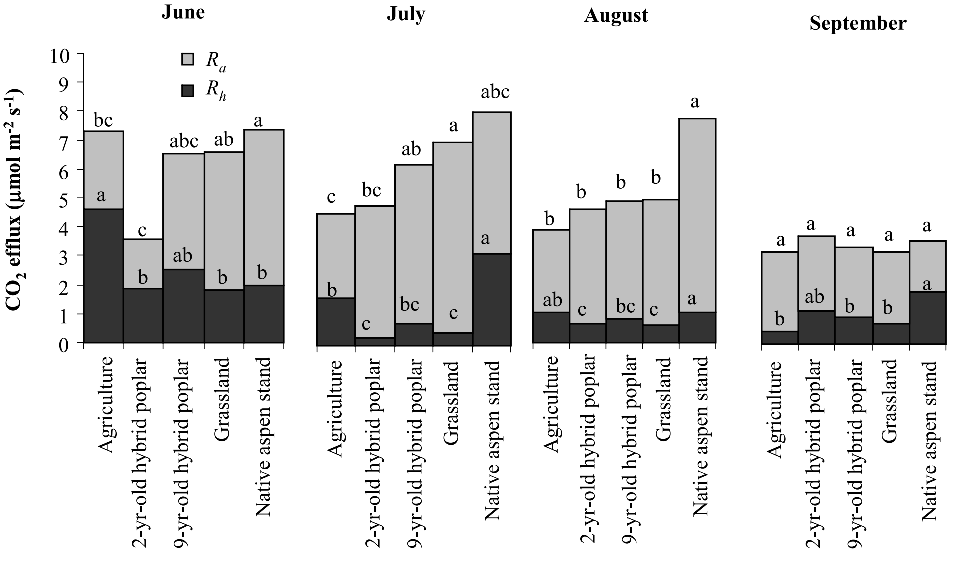

Figure 6. Mean monthly autotrophic (R_a) and heterotrophic (R_h) respiration in the 2006 growing season in various land uses in Linaria, Alberta. Different letters among land uses are significantly different at p value <0.05.

and 3.83 μmol CO_2 m^{-2} s^{-1}, respectively) than for the 2 year old hybrid poplar and agricultural sites (3.06 and 2.69 μmol CO_2 m^{-2} s^{-1}, respectively, Figure 6). R_a was positively correlated with the fine root biomass ($r = 0.44$); but negatively correlated with θ_v ($r = -0.81$) and available NO_3^- ($r = -0.92$) and P ($r = -0.94$).

4. Discussion

4.1. Seasonal Soil Respiration Under Different Land Uses

[28] Cumulative R_s for native aspen stand, and also for 2 and 9 year old hybrid poplar plantations, during the growing seasons compared well with values of 513–802 g C m^{-2} reported by *Tang et al.* [2009] for recently disturbed, young, intermediate, and mature aspen stands in Wisconsin and Michigan. Differences in cumulative R_s between the land uses were also related to the differences in aboveground, belowground, and total ecosystem C stocks observed in this study. Several studies [*Bond-Lamberty et al.*, 2004; *Raich and Tufekcioglu*, 2000] have suggested that R_s tend to be greater in sites with greater detritus, which provide substrates for heterotrophic activity. We found that aboveground and belowground biomass C stocks (and presumably detritus production) increased nine years after hybrid poplar plantations were established on agricultural land, and resulted in a 10% increase in cumulative R_s (Table 2). In the native aspen stand, the presence of snags, coarse woody debris, and the LFH layer represents greater surface C accumulation. Even if the productivity of the agricultural field was relatively high (17 Mg C ha^{-1} in total plant biomass), only a small portion of the biomass was left in the field after harvest (3 Mg C ha^{-1} in the form of fine roots and stubble). The higher amount of detritus accumulated on the soil surface in native aspen stand was reflected in a greater cumulative R_s, which was 55%, 82%, 42%, and 49% higher relative to the agricultural, 2 and 9 year old hybrid poplar and grassland sites, respectively.

[29] At the native aspen stand, we evaluated the relative contributions of the LFH layer and found that 75% of the efflux originated from this layer (Table 2). This agrees closely with *Khomik et al.* [2006] who used litter layer removal experiments to show that 62–85% of the R_s originated from the 12 to 20 cm thick LFH layer in a 74 year old boreal mixedwood forest in central Ontario, Canada; and with *Uchida et al.* [1998] who examined the vertical distribution of R_s and found that 50–60% of R_s originated in the FH layer in an 80 year old boreal forest dominated by black spruce with a few aspen trees in Saskatchewan, Canada.

[30] Cumulative seasonal soil C efflux via R_s in agriculture (502 g C m^{-2}, average for 2006 and 2007), was approximately 2.5 times higher than in the native aspen stand without the LFH layer ($R_{NAT\text{-}LFH} = 194$ g C m^{-2}) with a similar ratio for R_{sub} values (Table 2). The higher emissions of soil C under agriculture may be related to the land management because soil aeration and moisture become favorable for decomposition during cultivation. In addition, mixing of the soil also disrupts soil aggregates to further expose physically protected C to decomposition [*Six et al.*, 1998]. As much as 20–50% of initial soil organic C stocks from native soils have been reported to be lost due to cultivation [*Guo and Gifford*, 2002].

[31] The proportion of respiration originating from below 11 cm depth, R_{sub}, was highest (72%) in the agricultural field, intermediate in 2 year old hybrid poplar (49%), grassland (47%), and 9 year old hybrid poplar (39%) sites, and lowest (17%) in the native aspen stand. Higher R_{sub} in agriculture and 2 year old hybrid poplar plantation may be due to multiple tillage operations that occurred on the site for crop or plantation establishment and weed control which likely stimulated greater deeper root growth and turnover [*Ellert and Janzen*, 1999]. Site preparation in the 2 year old hybrid poplar plantation involved deep (25–30 cm) and shallow (10 cm) tillage the previous year while weed control involved two passes of shallow (10 cm) tillage at the beginning and end of each growing season. Lower R_{sub} in native aspen stand, on the other hand, may be attributed to unfavorable soil environment, namely, lower T_s (Figure 2), higher soil bulk density, and lower NO_3^- content [*Arevalo et al.*, 2009], as each of these factors would tend to reduce root and microbial activity and respiration and thus decrease R_{sub} [*Burton et al.*, 1997] compared to systems with soil cultivation.

[32] Vegetation cover can alter soil temperature and soil moisture conditions and thereby significantly influence soil respiration rates [*Raich and Tufekcioglu*, 2000]. We found that T_s in the native aspen stand was consistently lower compared to the agricultural field. This is likely due to the shading of trees and the presence of the LFH layer. The LFH layer acts as an insulating mulch to reduce heat gain (from solar radiation) during daytime and loss during nighttime and hence moderate temperature conditions. Our data clearly showed that R_s was highly correlated with T_s for both the native aspen and agricultural sites, both diurnally and seasonally (Table 2).

4.2. Diurnal Soil Respiration Under Different Land Uses

[33] R_s originating from the mineral soil (excluding the LFH layer in the native aspen stand) showed similar diurnal variations for all land use types with early morning (generally before 0900 h) minima and late afternoon (generally after 1500 h) maxima. This pattern persisted throughout the early, middle and late parts of the growing season. The diurnal minimum and peak R_s not only corresponded with variations in T_s but also were related to different growth stages of vegetation present at each site. For example, these values in general were highest in the middle of the growing season. Fine root growth, especially for hybrid poplar plantations, has been shown to begin early in the spring, increasing exponentially until the middle of the growing season, and decreasing in the fall and winter [*Coleman et al.*, 2000]. It was also shown that the majority (65%) of the hybrid poplar fine roots appeared during the growing season and while half of fine roots survived after 149 days only 6% remained after 700 days [*Coleman et al.*, 2000]. In an associated study [*Arevalo et al.*, 2009], we found that fine root biomass generally increased from June to October in the agricultural and 2 year old hybrid poplar sites and more than doubled by the end of the growing season, increased more than fivefold in the 9 year old hybrid poplar plantation but increased by only 39% in the grassland site. This growth pattern for fine roots may partially explain the increase in R_s from the early to middle parts of the growing season. In the

fall, R_s decreased, presumably resulting from decreasing root biomass production and lower T_s. Comparing the two hybrid poplar plantations in mid-July (Figure 5), R_s was highest at the 9 year old compared to the 2 year old hybrid poplar plantation. This may be attributed to higher fine root biomass in the 9 year (614 g C m^{-2}) as compared to the 2 year old hybrid poplar plantation (230 g C m^{-2}).

4.3. Heterotrophic Soil Respiration

[34] On average, R_h accounted for approximately 25% of R_s across all land uses during the growing season. Although not statistically different across land uses, the agricultural site had the highest R_h/R_s ratio (0.35), followed by the native aspen stand (0.33) > 2 and 9 year old hybrid poplar plantations (0.26 and 0.25, respectively) > grassland (0.17). According to literature reviews [*Hanson et al.*, 2000; *Subke et al.*, 2006], R_h and R_a generally account for approximately one half of R_s each. However, these averages mask considerable variation due to the vast diversity of ecosystems and potential biases of different partitioning techniques and timescales. The partitioning method (root exclusion) we used involved severing (but not removing) all the roots around the perimeter of collars in order to eliminate root respiration and inhibit future root growth. One limitation of this technique is that cessation of root activity within the collars would have eliminated transpiration losses resulting to possibly higher soil moisture, which may in turn, affect decomposition [*Hanson et al.*, 2000] and potentially overestimate R_h (or underestimate R_a) in our calculations. Another limitation of this technique is that we took our first measurements one month after the long collars were established. This may not have been enough time for R_h from dying roots to disappear and may cause R_h to be overestimated. Another complicating factor of this technique is the presence of roots below the root-exclusion zone, i.e., below 30 cm depth; and the possibility of roots growing into the root-exclusion zone from the bottom [*Hanson et al.*, 2000]. We determined fine root distribution in the 0–30 cm soil profile during one of the sampling periods (data not shown) and found that fine root biomass decreased with depth (0–10 cm: 55%; 10–20 cm: 32%; 20–30 cm: 13%) in all land uses. However, we were not able to quantify whether and to what extent possible artifacts related to root biomass below the root-exclusion zone affected R_s. Therefore a more detailed investigation into the changes in soil conditions following root exclusion is necessary to estimate proportions of R_h and R_a more accurately.

[35] The quality of soil organic C (as determined by the natural abundance of ^{13}C) under different land uses could be related to its decomposability [*Ehleringer et al.*, 2000] and its sensitivity to T_s (as determined by its Q_{10} values). A more enriched (less negative) ^{13}C value indicates a more stabilized (less labile) form of C. The more stable the C, the lower its lability and temperature sensitivity (Q_{10} value). In an associated study [*Arevalo et al.*, 2009], we found decreasing ^{13}C abundance in the 0–10 cm mineral soil layer in the order of: native aspen > grassland > 9 year old hybrid poplar > 2 year old hybrid poplar > agriculture ($\delta\ ^{13}$C values of −26.24 ‰, −26.77 ‰, −26.83 ‰, −27.37 ‰, and −27.78 ‰, respectively). These results suggest that soil organic C in the native aspen stand had the highest proportion of the humified form compared to the other sites. Conversely, the agricultural site had the highest proportion of the labile C, with grassland and 2 and 9 year old hybrid poplar sites having intermediate levels of humified and labile C forms. In addition, we found that Q_{10} values were in the order of: agriculture > 2 year old hybrid poplar > 9 year old hybrid poplar > native aspen > grassland (Table 1), which means that soil organic matter in the agricultural field is most sensitive to changes in T_s, intermediate under the hybrid poplar systems, and least under the native aspen stand and grassland systems. A comparison of cumulative C efflux in the native aspen stand and other land uses (Table 2) indicates that the majority of R_s in the former originated from labile C in the LFH layer. A more enriched form of ^{13}C and somewhat lower Q_{10} for mineral soil in the native aspen stand is indicative of stabilized C translocated from the upper layer. On the other hand, lower values of ^{13}C and higher values of Q_{10} under agriculture and 2 year old hybrid poplar plantation suggest the presence of more labile C forms in these systems. This may be responsible for greater R_s in these ecosystems as fresh litter was mixed up in the upper 30 cm layer during tillage operations.

4.4. Autotrophic Respiration

[36] Our estimates of R_a/R_s (65–83%) were slightly higher in comparison to other published studies involving trenched plots, namely, 37% in the work of *Saurette et al.* [2008], 35–70% in the work of *Lavigne et al.* [2003], and 27–71% in the work of *Lee et al.* [2003]. Lower estimates of R_a could have been due to the contribution from decomposition of severed roots [*Ohashi et al.*, 2000], and lateral diffusion of CO_2 from the control to the root exclusion plot at its base [*Jassal and Black*, 2006]. In a review involving 54 sites, *Bond-Lamberty et al.* [2004] proposed a global relationship between R_s and R_a ($R_a^{0.5} = -7.57 + 0.93R_s^{0.5}$; $r^2 = 0.87$). Our cumulative R_a was higher than the global relationship proposed by *Bond-Lamberty et al.* [2004], but fell within the 95% confidence interval of this global relationship.

[37] The proportion of R_a to R_s decreased in the order of: native aspen > grassland > 9 year old hybrid poplar > agriculture > 2 year old hybrid poplar (Table 2) and was related to fine root biomass ($r = 0.79$). Aside from fine root biomass, R_a is also related to nutrient availability, specifically NO_3^- ($r = -0.92$) and P ($r = -0.94$), and soil moisture content ($r = -0.81$). Based on the inverse relationship, it seems reasonable to hypothesize that fine root biomass was inversely related to NO_3^- and P availability on these sites. With limited supply of nutrients, plants tend to allocate more biomass to fine roots which in turn increases R_a. Availability of limiting nutrients has been suggested to be the major factor governing biomass allocation patterns in plants [*Vogt et al.*, 1985].

5. Conclusions

[38] Changes in land use led to differences in annual input of plant litter to the soil, and aboveground and belowground biomass. In addition, the change in land use altered the microenvironmental conditions of the soil, which is known to affect litter decomposition rates and ultimately the quality and quantity of soil organic matter. The conversion of a

native forest to agricultural land resulted in the loss of the surface organic layer, which is the primary location of R_s in natural forest ecosystems in boreal regions. The results highlighted the importance of discerning R_s as a product of the production and consumption of organic matter that are inextricably linked to and influenced by a variety of controlling factors. Soil surface CO_2 flux was lower in the 2 year old hybrid poplar plantation resulting from lower fine root biomass (and thus lower R_a), although this was somewhat offset by slightly higher R_h due to higher T_s. Higher soil surface CO_2 flux in the 9 year old hybrid poplar plantation and grassland was due to greater fine root biomass that increased R_a as well as higher rates of litter inputs to support heterotrophs. It is thus important to consider the alterations in the relationship between R_s and environmental factors, brought about by land use change, when estimating variations in the C cycle and its response to future climate change.

Notation

D_a	molecular diffusivity of CO_2 in air, $m^2\ s^{-1}$.
D_{a0}	CO_2 diffusivity in air at 293.15 K and 101.3 kPa, given as 14.7 $mm^2\ s^{-1}$.
D_i	diffusivity of CO_2 in the soil, $m^2\ s^{-1}$, at depth *i*.
F_i	soil CO_2 flux, $\mu mol\ m^{-2}\ s^{-1}$, at depth *i*.
P	air pressure, kPa.
Q_{10}	relative increase in R_s for every increase of 10°C in T_s.
R_a	rate of CO_2 efflux originating from autotrophic respiration, $\mu mol\ m^{-2}\ s^{-1}$.
R_h	rate of CO_2 efflux originating from heterotrophic respiration, $\mu mol\ m^{-2}\ s^{-1}$.
$R_{NAT\text{-}LFH}$	rate of CO_2 efflux under the LFH (litter-fibric-humus) layer, $\mu mol\ m^{-2}\ s^{-1}$.
R_s	rate of total CO_2 efflux at the soil surface, $\mu mol\ m^{-2}\ s^{-1}$.
R_{sub}	rate of CO_2 efflux at 11 cm depth, $\mu mol\ m^{-2}\ s^{-1}$.
T_s	soil temperature, °C.
T_a	air temperature, K.
$\partial C/\partial z$	vertical soil CO_2 concentration gradient, $\mu mol\ m^{-4}$.
$\delta^{13}C$	natural abundance of ^{13}C, ‰.
ε	soil air-filled porosity, $m^3\ m^{-3}$.
θ_v	soil volumetric water content, $m^3\ m^{-3}$.
ξ	gas tortuosity factor.
ρ_b	soil bulk density, $kg\ m^{-3}$.
ρ_m	soil particle density, $kg\ m^{-3}$.
φ	total soil porosity, m^3 air m^{-3} soil.

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