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Authors

Coursolle, C.
Margolis, H.A.
Giasson, M.-A.
[et al.](#)

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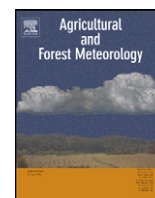
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Influence of stand age on the magnitude and seasonality of carbon fluxes in Canadian forests

C. Coursolle^{a,*}, H.A. Margolis^a, M.-A. Giasson^{a,1}, P.-Y. Bernier^b, B.D. Amiro^c, M.A. Arain^d, A.G. Barr^e, T.A. Black^f, M.L. Goulden^g, J.H. McCaughey^h, J.M. Chenⁱ, A.L. Dunn^{j,2}, R.F. Grant^k, P.M. Lafleur^l

^a Centre d'étude de la forêt, Faculté de foresterie, de géographie et de géomatique, 2405 rue de la Terrasse, Université Laval, Québec, QC G1V 0A6, Canada

^b Canadian Forest Service, 1055 rue du P.E.P.S., C.P. 10380, Succ. Ste-Foy, Québec, QC G1V 4C7, Canada

^c Department of Soil Science, University of Manitoba, Winnipeg, MB R3T 2N2, Canada

^d School of Geography and Earth Sciences and McMaster Centre for Climate Change, 1280 Main Street, McMaster University, Hamilton, ON L8S 4K1, Canada

^e Environment Canada, 11 Innovation Boulevard, Saskatoon, SK S7N 3H6, Canada

^f Faculty of Land and Food Systems, 2357 Main Mall, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

^g Department of Earth System Science, University of California, Irvine, CA 92697-3100, USA

^h Department of Geography, Queen's University, Kingston, ON K7L 3N6, Canada

ⁱ Department of Geography and Program in Planning, University of Toronto, 100 George Street, Toronto, ON M5S 3G3, Canada

^j Department of Earth and Planetary Sciences, Harvard University, 29 Oxford Street, Cambridge, MA 02138, USA

^k Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2E3, Canada

^l Department of Geography, Trent University, Peterborough, ON K9J 7B8, Canada

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ABSTRACT

Proper management and accounting of forest carbon requires good knowledge of how disturbances and climate affect the carbon dynamics of different stand types. We have investigated such relationships by measuring, over a 5-year period (2003–2007), the net ecosystem productivity (NEP), gross ecosystem productivity (GEP) and ecosystem respiration (ER) of 26 forest sites in Canada using the eddy covariance technique. The study included black spruce, jack pine, Douglas-fir, aspen, boreal mixedwood and white pine forest ecosystems ranging in age from 1- to 153-years. The dataset included six chronosequences (one afforested plantation, three harvested and two burned).

Following planting, the afforested white pine stands quickly became carbon sinks and offset initial carbon losses after 4 years. Depending on forest type, the other forest stands were carbon sources for 10–18 years following a disturbance, offset initial carbon losses after 19–47 years, and showed net total gains ranging from 38 to 86 Mg C ha⁻¹ at 80 years. Peak NEP ranged from 0.9 to 2.9 Mg C ha⁻¹ year⁻¹ at ages of 35–55 years except for the afforested white pine where it was 6.9 Mg C ha⁻¹ year⁻¹ at 15–20 years. Stepwise regression and Pearson correlation analyses indicated that the GEP and ER of mature stands (>70 years old) were driven mainly by climate, while fluxes of young stands (<19 years old) were driven by both leaf area index and climate.

Although stand age of the afforested white pine plantations did not affect the GEP growing season lengths, the growing season length of the other forests increased with age until about 20 years and this coincided with the switch from carbon source to sink. With the exception of the afforested white pine, peak GEP/ER ratios of the youngest sites occurred later in the growing season compared to older sites. The strong influence of stand age on the seasonal dynamics of GEP fluxes needs to be considered to avoid confounding the impacts of climate change with those of disturbance. These age-related seasonality effects are continental in scope and should be important in interpreting the time series of atmospheric CO₂ concentration measurements at regional and global scales.

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1. Introduction

Anthropogenic greenhouse gas emissions have been increasing since the beginning of the industrial age and the resulting increase in atmospheric CO₂ concentrations are now widely believed to be changing the planet's climate. The Earth's terrestrial and ocean ecosystems have been sequestering a large portion of these CO₂ emissions (Canadell et al., 2007a; Sarmiento and Gruber, 2002). By

* Corresponding author. Tel.: +1 418 656 2131x8370; fax: +1 418 656 5262.

E-mail address: carole.coursolle@sbf.ulaval.ca (C. Coursolle).

¹ Current address: Department of Biology, Boston University, Boston, MA 02215, USA.

² Current address: Department of Physical & Earth Sciences, Worcester State University, 486 Chandler St., Worcester, MA 01602, USA.

constraining the increases in atmospheric CO₂ concentrations with the observations of a weak north-south concentration gradient, Tans et al. (1990) concluded that there was a northern extratropical net carbon sink of ~2 Pg C year⁻¹. Later studies suggest that the efficiency of the terrestrial carbon sink has been decreasing due to changes in the Earth's climate (Canadell et al., 2007b).

The spatial distribution of the terrestrial sink has been the subject of significant debate over recent years (Canadell and Raupach, 2008; Ciais et al., 2010; Le Quéré et al., 2007, 2009; Rödenbeck et al., 2003; Stephens et al., 2007) and the current and future role of northern forests in the terrestrial sink is still an active research question (Ciais et al., 2010). Using forest inventory data and long-term ecosystem carbon studies, Pan et al. (2011) concluded that boreal forests accounted for 21% (0.50 ± 0.08 Pg C year⁻¹) of the overall global carbon sink from established forests (2.41 ± 0.42 Pg C year⁻¹) between 1990 and 2007. Overall, the boreal carbon sink over this time period was found to be the sum of a reduction in Canadian forest carbon stocks due to disturbance that was offset by an increasing biomass sink in other boreal regions. Clearly ecological disturbance and forest management are having a major influence on the contribution of boreal forests to global carbon sequestration (Kurz et al., 2008a,b,c). It is also well recognized that northern forests contain large amounts of carbon (C) in both biomass and soils (Kurz and Apps, 1995, 1999; Tarnocai et al., 2009) and these reservoirs may be even more vulnerable to future changes in climate. Since Canada contains 10% of the world's forests, proper accounting and management of these large C stocks requires a solid scientific understanding of how disturbance and climate variability impact the emission and sequestration of carbon by these forests and how we might separate the effects of these two factors on regional C budgets.

Eddy covariance (EC) flux towers are one of the main tools used to monitor, understand and quantify CO₂ exchange between forests and the atmosphere (Baldocchi, 2008) because they provide near-continuous half-hourly time series of carbon, water, and energy exchange at the ecosystem scale. Regional networks of flux towers have been developed over the last two decades in different parts of the world. In Canada, the Fluxnet-Canada Research Network (2002–2007) and the follow-on Canadian Carbon Program (2007–2011) Research Network have had a leadership role in the study of the C cycle of Canada's forests and peatlands, as affected by disturbances and climate variability (Margolis et al., 2006). Amiro et al. (2010) presented an overview of how fire, harvest, windthrow, insects, and silvicultural treatments influence C exchange in North American forest ecosystems.

In this study, we focus on a continental-scale transect of forest flux towers across Canada to address how disturbance types, stand age and climate variability may impact the C exchange of northern and coastal forests. We use six different chronosequences to determine: (1) the age at which forests reach the C compensation point when they switch from a C source to a C sink, and the offset point when carbon sequestration equals carbon loss following disturbance or afforestation, (2) the influence of stand age on the seasonal dynamics of the fluxes, and (3) the extent to which climate versus stand structure are the main drivers of interannual variability following disturbance.

2. Materials and methods

2.1. Fluxnet-Canada and the Canadian Carbon Program

The Fluxnet-Canada Research Network (FCRN) was established in 2002 and consisted of a series of eddy-covariance flux towers installed in mature and disturbed forests as well as peatlands across the country. Continuous year-round measurements of

carbon, water and energy exchanges between the land surface and the atmosphere were made using standard measurement protocols. The FCRN was the next logical step in the study of the interactions between Canadian forests and the atmosphere, following the Boreal Ecosystem-Atmosphere Study (BOREAS) which was carried out between 1994 and 1996 (Sellers et al., 1997). The FCRN was established using the main flux tower sites from BOREAS in Saskatchewan (which had become the Boreal Ecosystems Research and Monitoring Sites (BERMS) program) and Manitoba, as well as a few other existing sites, to which new sites were added so as to produce an east-west transect across Canada. Several chronosequences were included in the transect, facilitating the study of disturbance effects and stand age on the carbon cycle. The FCRN was succeeded in 2007 by the Canadian Carbon Program (CCP).

2.2. Study sites

The description and characteristics of the 26 forests sites, ranging in age from 1- to 153-years old, used in this study are given in Tables 1 and 2. Sixteen of these sites were supported by the FCRN/CCP (Coursolle et al., 2006; Margolis et al., 2006), four (WP39-ON, WP74-ON, WP89-ON, WP02-ON) were FCRN/CCP associated sites (Peichl and Arain, 2006), and six (BS1850-MB, BS30-MB, BS64-MB, BS81-MB, BS89-MB, BS98-MB) were part of the Ameriflux network (Goulden et al., 2006). The study, which included two burn chronosequences (BBS-MB, BJP-SK), three harvested chronosequences (HBS-QC, HDF-BC, HJP-SK) and an afforested plantation chronosequence (PWP-ON), was comprised of 10 black spruce (BS), seven jack pine (JP), three Douglas-fir (DF) and four white pine stands (WP), and one each of aspen (ASP) and a mixedwood stand (MW). Sites within a chronosequence were similar in climate, soil characteristics, disturbance history and topography (Goulden et al., 2006). Measurements were available for periods ranging from 2.5 to 5 years, with 50% of the sites having a full 5 year measurement record.

2.3. Measurements and data analysis

Meteorological and flux data for 105 site-years were obtained from either the FCRN Data Information System (<http://fluxnet.ccrp.ec.gc.ca>) or directly from Principal Investigators (PIs). Half-hourly C fluxes were measured using the EC technique (Aubinet et al., 2000; Morgenstern et al., 2004) and, with the exception of the BBS-MB chronosequence, were processed following FCRN protocols (Coursolle et al., 2006; Zha et al., 2009). Net ecosystem exchange (NEE) was computed as $NEE = F_c + S_c$, where F_c is the measured C flux and S_c is the rate of change in CO₂ storage between the measurement height and the ground. Depending on the site, F_c was measured using either a closed- or open-path infrared gas analyzer (IRGA). S_c was computed using a multi-level CO₂ concentration measurement system when available, or as a one-level storage term calculated using the CO₂ concentration measured by the EC IRGA. Initial quality control of all half-hourly data was carried out by each site's PI. With the exception of the BBS-MB chronosequence, cross-validation of meteorological and eddy-covariance equipment was carried out as part of FCRN quality assurance activities using a standard set of roving flux and meteorological calibration equipment.

Night-time measurements were eliminated when atmospheric conditions were calm. These conditions were identified when the measured friction velocity (u_* , m s⁻¹) was lower than the site-specific threshold (u_{*th}). The threshold was estimated for each site by plotting nighttime NEE against u_* and selecting the minimum u_* value (aggregated in 0.05 m s⁻¹ bins) when NEE was no longer dependent on u_* (Humphreys et al., 2006). Moreover, NEE outliers (30-min fluxes farther than four standard deviations away from

Table 1
List of Canadian flux sites used in this study.

Site	Age class ^b	Alternate site name ^c	Data availability	Location (latitude/longitude)	Reference
<i>HJP-SK</i> ^a					
OJP-SK	MAT	SK-OldJackPine	2003–2007	53.9°N/104.7°W	Zha et al. (2009)
HJP75-SK	INT	SK-HarvestJP1975	May 2004–2007	53.9°N/104.6°W	Zha et al. (2009)
HJP94-SK	YNG	SK-HarvestJP1994	2003–2005	53.9°N/104.7°W	Zha et al. (2009)
HJP02-SK	YNG	SK-HarvestJP2002	July 2003–2007	53.9°N/104.6°W	Zha et al. (2009)
<i>BJP-SK</i> ^a					
OJP-SK ^d	MAT	SK-OldJackPine	2003–2007	53.9°N/104.7°W	Zha et al. (2009)
F77-SK	INT	SK-Fire1977	August 2003–2006	54.5°N/105.9°W	Mkhabela et al. (2009)
F89-SK	YNG	SK-Fire1989	2003–2005	54.3°N/105.9°W	Mkhabela et al. (2009)
F98-SK	YNG	SK-Fire1998	2003–2006	53.9°N/106.1°W	Mkhabela et al. (2009)
<i>HBS-QC</i> ^a					
EOBS-QC	MAT	QC-MatureBlackSpruce	July 2003–2007	49.7°N/74.3°W	Bergeron et al. (2008)
HBS00-QC	YNG	QC-BSpruceJPineCut	2003–2007	49.3°N/74.0°W	Giasson et al. (2006)
<i>BBS-MB</i> ^a					
BS1850-MB	MAT	UCI 1850	2003–August 2005	55.9°N/98.5°W	Goulden et al. (2006)
BS30-MB	MAT	UCI 1930	2003–August 2005	55.9°N/98.5°W	Goulden et al. (2006)
BS64-MB	INT	UCI 1964	2003–August 2005	55.9°N/98.4°W	Goulden et al. (2006)
BS81-MB	INT	UCI 1981	2003–August 2005	55.9°N/98.5°W	Goulden et al. (2006)
BS89-MB	YNG	UCI 1989	2003–August 2005	55.9°N/99.0°W	Goulden et al. (2006)
BS98-MB	YNG	UCI 1998	2003–August 2005	56.6°N/99.9°W	Goulden et al. (2006)
<i>HDF-BC</i> ^a					
DF49-BC	INT	BC-DFir1949	2003–2007	49.9°N/125.3°W	Humphreys et al. (2006)
HDF88-BC	YNG	BC-HarvestDFir1988	2003–2007	49.5°N/124.9°W	Humphreys et al. (2006)
HDF00-BC	YNG	BC-HarvestDFir2000	2003–2007	49.9°N/125.3°W	Humphreys et al. (2006)
<i>PWP-ON</i> ^a					
WP39-ON	INT	ON-PlantnWPine1939-TP	2003–2007	42.7°N/80.4°W	Arain and Restrepo-Coupe (2005)
WP74-ON	INT	ON-PlantnWPine1974-TP	2003–2007	42.7°N/80.3°W	Peichl and Arain (2006)
WP89-ON	YNG	ON-PlantnWPine1989-TP	2003–2007	42.8°N/80.5°W	Peichl and Arain (2006)
WP02-ON	YNG	ON-PlantnWPine2002-TP	2003–2007	42.7°N/80.6°W	Peichl and Arain (2006)
<i>Non-Chrono</i> ^a					
SOBS-SK	MAT	SK-OldBlackSpruce	2003–2007	54.0°N/105.1°W	Krishnan et al. (2008)
NOBS-MB	MAT	MB-NOldBlackSpruce	2003–2007	55.9°N/98.5°W	Dunn et al. (2007)
OMW-ON	MAT	ON-OldMixedWood-GhogR	September 2003–2006	48.2°N/82.2°W	McCaughy et al. (2006)
OA-SK	MAT	SK-OldAspen	2003–2007	53.7°N/106.2°W	Krishnan et al. (2006)

^a HJP-SK: harvested jack pine in Saskatchewan; BJP-SK: burned jack pine in Saskatchewan; HBS-QC: harvested black spruce in Quebec; BBS-MB: burned black spruce in Manitoba; HDF-BC: harvested Douglas-fir in British Columbia; PWP-ON: afforested white pine plantations in Ontario; Non-Chrono: single sites not belonging to a chronosequence.

^b MAT: mature stands (73–153 years old in 2003); INT: intermediate-aged stands (22–64 years old in 2003); YNG stands: (1–15 years old in 2003).

^c Site names in Fluxnet-Canada or Ameriflux databases.

^d The same site is used for both the HJP-SK and the BJP-SK chronosequences.

the monthly mean) were eliminated except for the SK-HJP02 site where most of the outliers were retained because they are believed to be caused by atmospheric gravity waves.

Net ecosystem productivity (NEP), which was calculated as $NEP = -NEE$, is positive when CO_2 is sequestered by the ecosystem (sink) and negative when CO_2 is emitted to the atmosphere (source). Data gaps in CO_2 fluxes were filled and ecosystem respiration (ER) and gross ecosystem productivity (GEP) were estimated following the standard FCRN gap-filling procedure (Barr et al., 2004; Amiro et al., 2006) for all sites with the exception of WP74-ON, WP89-ON, WP02-ON, F77-SK, F89-SK and F98-SK. The FCRN procedure uses a three-parameter logistic equation relating ER to soil temperature, the Michaelis–Menten equation to relate GEP to PPFD and a 100-point moving window to allow certain parameters (e.g. A_{max}) to vary over time. The gap-filling procedure used for WP74, WP89, WP02 sites is described in Peichl et al. (2010a,b). The use of open-path analysers at the F77, F89 and F98 sites posed challenges during cold weather. Although there is a known heating issue with these analysers (Burba et al., 2008), Amiro (2010) demonstrated that the heating corrections were not a satisfactory solution for this data set, and that gap-filling winter data with respiration functions was the best solution. Open-path analysers were also used at the HBS00-QC and the HJP02-SK (for July 2003–November 2004 period only) but sensor heating issues were not observed at either of these cutover sites.

The photosynthetic growing season was identified using non-gapfilled GEP, except for the WP74-ON, WP89-ON and WP02-ON sites where gapfilled GEP was used instead because of the presence of large data gaps (several weeks in length). Five-day running means of GEP were calculated for each data set and a yearly maximum was identified for each site. The beginning of each growing season was identified as the first occurrence of five consecutive days with a GEP running mean greater than 15% of the yearly daily maximum GEP. The end of the growing season was identified as the first occurrence when the GEP running mean fell below 15% of the maximum value for five consecutive days during the calendar year. This method is similar to that used by McMillan et al. (2008) and Zha et al. (2009). Using non-gapfilled GEP data was the preferred method in our case so as to avoid any influence of the gapfilling algorithm which set GEP to 0 when site temperatures fell below specific thresholds and we used 5-day running means to ensure that each half-hour of the day was represented in the calculation of mean daily GEP. The 15% threshold was selected after analyzing the results obtained using various thresholds (5–20%) and best identified the period of continuous photosynthesis at all sites as well as spring ramp-up, and corresponded well with the end of the snow cover period.

To identify periods with snow cover, we first calculated the mean value of the ratio of upward to downward photosynthetic photon flux density (PPFD) for each day using only daytime data. A

Table 2
Summary description of flux sites used in this study.

	TSD/age (years) ^a	T _a (°C) ^b	Stand origin	LAI (m ² m ⁻²)	AGB (kg C m ⁻²) ^c	Dom. species ^d
<i>HJP-SK</i>						
HJP75-SK	28	1.2	Harvest	2.9	2.11	JP
HJP94-SK	9	1.9	Harvest	1.1	0.17	JP
HJP02-SK	1	0.3	Harvest	0.2	0.03	JP
<i>BJP-SK</i>						
OJP-SK	88	2.3	Fire	1.9–2.0	3.98	JP
F77-SK	26	0.7	Fire	3.4	1.81	JP, BS
F89-SK	14	0.1	Fire	3	2.27	JP, TA, BS
F98-SK	5	2.0	Fire	1.1	4.00	JP, BS, TA
<i>HBS-QC</i>						
EOBS-QC	100	0.9	Fire/harvest	3.7	4.50	BS
HBS00-QC	3	1.2	Harvest	0.7–1.5	0.15	KA, VA, BS, JP
<i>BBS-MB</i>						
BS1850-MB	153	-2.3	Fire	5.7	9.00	BS
BS30-MB	73	0.2	Fire	7.8	7.01	BS
BS64-MB	39	-2.7	Fire	5.3	3.62	BS, JP, TA
BS81-MB	22	-2.5	Fire	5.5	2.39	BS, JP, TA
BS89-MB	14	-2.2	Fire	3	0.29	BS, JP, TA
BS98-MB	5	-3.3	Fire	1.4	N/A	LT, WR, GA, WI
<i>HDF-BC</i>						
DF49-BC	54	8.6	Harvest	7.3	13.81	DF
HDF88-BC	15	9.7	Harvest	3.9–6.7	1.14	DF
HDF00-BC	3	9.1	Harvest	1.8–2.3	0.17	DF
<i>PWP-ON</i>						
WP39-ON	64	8.6	Afforest	8.0	10.94	WP
WP74-ON	29	8.8	Afforest	5.9	5.04	WP
WP89-ON	14	8.5	Afforest	12.8	3.14	WP
WP02-ON	1	8.7	Afforest	0.5–2.7	0.09	WP
<i>Non-Chrono</i>						
SOBS-SK	123	1.9	Fire	3.8	4.92	BS
NOBS-MB	153	-0.4	Fire	4.8	5.72	BS
OMW-ON	74	3.4	Harvest ^e	4.3	6.78	TA, BS, WS, WB, BF
OA-SK	84	2.6	Fire	1.9–2.5	7.88	TA

^a Time since disturbance/approximate age of stand in 2003.

^b Mean annual air temperature based on full years of available data for each site.

^c Above-ground live biomass.

^d Dominant species: BF: balsam fir (*Abies balsamea* (L.) Mill.), BP: balsam poplar (*Populus balsamifera* L.), BS: black spruce (*Picea mariana* (Mill.) BSP), DF: Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), JP: jack pine (*Pinus banksiana* Lamb.), KA: *Kalmia augustifolia* L., LT: Labrador tea (*Ledum groenlandicum* Oeder), GA: green alder (*Alnus crispa* (Aiton) Pursh), TA: trembling aspen (*Populus tremuloides* Michx.), TM: tamarack (*Larix laricina* (Du Roi) K. Koch), VA: *Vaccinium angustifolium* L., WB: white birch (*Betula papyrifera* Marsh.), WI: willow (*Salix* L.), WP: white pine (*Pinus strobes* L.), WR: wild rose (*Rosa* spp.), WS: white spruce (*Picea glauca* (moench) Voss).

^e High-grading.

threshold specific to each site was identified above which the day was considered to have snow on the ground. Snow cover periods were identified when there were at least five consecutive days with the ratio greater than the threshold. When multiple periods existed within a calendar year (e.g. at the beginning and end of the snow season), the periods were merged together if they were separated by less than 15 days. When no upward PPFD data were available, we used near-surface soil temperature measurements. When possible, the snow cover periods identified using these criteria were validated using other data such as snow depth.

A robust nonlinear regression analysis conducted in MATLAB (The MathWorks Inc., Natick, MA) was used to predict annual net ecosystem production ($NEP_p = a * \exp(b * \text{age}) + c * \exp(d * \text{age})$), C losses and net gains at age 80 years, and the carbon compensation (C_{pt}) and offset (C_{off}) points for specific chronosequences and ecosystems. The BS-QC chronosequence was not used for this analysis because it was composed of only two sites. Following Dragoni et al. (2007), the uncertainties for the total C loss (cumulative NEP_p from age 1 to C_{pt}) and net C gain (cumulative NEP_p at age 80 years) estimates were calculated using a Monte Carlo simulation. An estimate of the random error (ϵ_s) was generated using a normal distribution with a mean of 0 and a standard deviation equal to the standard deviation of each NEP_p as generated by the regression model. Simulated values of NEP were then calculated as $NEP_s = NEP_p + \epsilon_s$. The

simulation was repeated 10,000 times and cumulative C losses and gains were then calculated for each simulation and the uncertainty of the net C loss and net C gains was estimated by calculating the standard deviation of the simulated summations.

Forward stepwise linear regressions (using $p = 0.05$ for entry into the model) and Pearson correlations performed by SAS (SAS Institute, Cary, NC) were used to identify variables having the greatest effect on annual GEP, ER and NEP. All other regressions were performed using SigmaPlot (Systat Software, Inc., Chicago, IL).

3. Results and discussion

3.1. Source/sink transition age and carbon offset point

Fig. 1a shows the composite picture of annual NEP as a function of age since disturbance or afforestation, for all stands in this study. Estimates of NEP obtained from exponential curves fit to the data from subsets of this full dataset indicate that the number of years needed to reach the C compensation point, the amount of carbon lost during this period and the time it takes to offset initial C losses, all depend on the stand type (Table 3). This curve-fitting exercise indicates that, generally, boreal forests in Canada are C sources for the first 9 years of growth and offset initial losses at

Table 3 Results from nonlinear regression analyses of annual NEP versus age since disturbance data in Fig. 1. Model used: $NEP_p = a * exp^{(b * age)} + c * exp^{(d * age)}$. Only significant results are shown. Values in parentheses are standard deviations. Models were fit to chronosequences having at least three sites.

Data set ^a	Model coefficients ^b				RMSE (Mg C ha ⁻¹ year ⁻¹) ^c	p	C comp Pt (years) ^d	Total C loss (Mg C ha ⁻¹) ^e	C offset Pt (years) ^f	Year peak NEP ^g	Peak NEP (Mg C ha ⁻¹ year ⁻¹) ^g	Net C gain at 80 years (Mg C ha ⁻¹)
	a	b	c	d								
Forests	19.693	-0.0272	-19.877	-0.0279	0.90	<0.0001	13	9.5(0.8)	28	49	1.37(0.20)	65.9(1.6)
Boreal	119.64	-0.0068	-382.94	-0.1235	0.64	<0.0001	10	9.1(0.8)	26	35	0.89(0.19)	44.4(1.4)
HJP-SK	28.742	-0.0376	-28.973	-0.0382	0.37	<0.0001	14	12.2(0.8)	34	40	0.98(0.30)	38.1(2.2)
BBS-MB	-19.781	-0.0220	19.682	-0.0215	0.69	<0.0001	10	3.7(1.8)	19	55	1.49(0.40)	81.9(3.4)
HDF-BC	-23.332	-0.0349	22.455	-0.0328	0.76	<0.0001	18	60.3(2.5)	47	47	2.92(1.0)	86.3(12.1)
PWP-ON	4209.7	-0.0528	-4552.7	-0.0878	1.60	<0.0001	3	2.1(1.5)	4	17	6.94(0.66)	270(6.5)

^a Forests: all sites except PWP-ON chronosequence sites; Boreal: all sites except PWP-ON and HDF-BC chronosequence sites. The regression for the burned jack pine chronosequence (BJP-SK) was not significant and is therefore not included in the table. A regression for the HBS-QC chronosequence was not calculated since only two age points were available.
^b Annual NEP in g m⁻² year⁻¹ was used for the model, model results (excepting coefficients) were converted to Mg ha⁻¹ year⁻¹.
^c Root mean square error of the model.
^d Age when sites are predicted to become C sinks.
^e Total C lost as predicted by the model (cumulative NEP from age 0 to carbon compensation point).
^f Age when C accumulation is predicted to offset initial carbon loss (age when cumulative NEP=0).
^g Age at which maximum NEP occurs, and maximum NEP as predicted by the model.

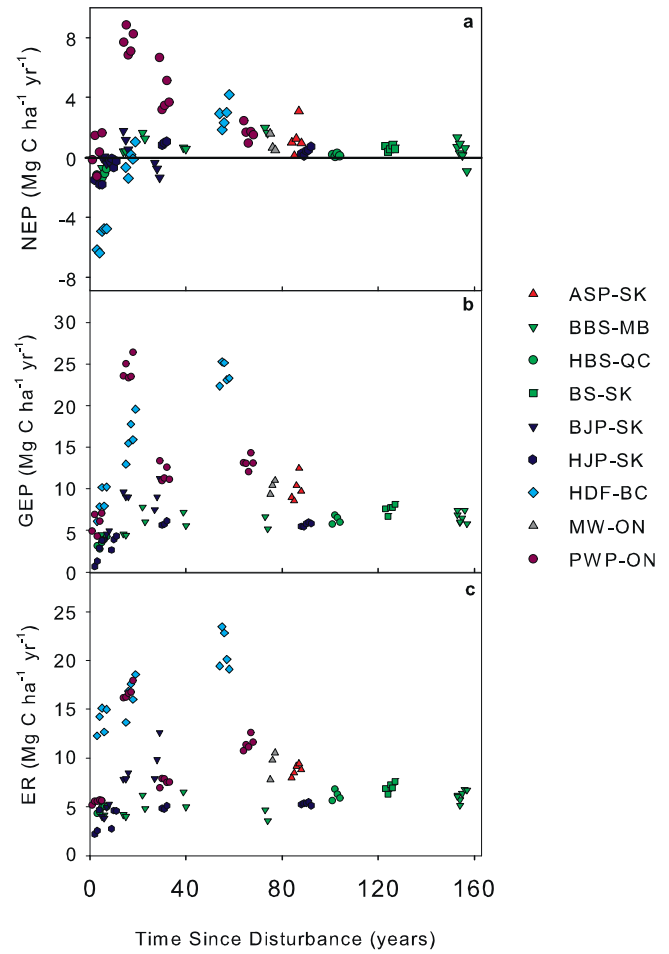


Fig. 1. Annual NEP (a), GEP (b) and ER (c) with respect to time since disturbance. Estimated uncertainties for NEP ranged from 4 to 10 g C m⁻² year⁻¹ for OA-SK, 4 to 65 g C m⁻² year⁻¹ for BBS-MB, 2 to 11 g C m⁻² year⁻¹ for HBS-QC, 3 to 9 g C m⁻² year⁻¹ for BS-SK, 50 g C m⁻² year⁻¹ for BJP-SK, 1 to 48 g C m⁻² year⁻¹ for HJP-SK, 2 to 14 g C m⁻² year⁻¹ for HDF-BC, 8 to 34 g C m⁻² year⁻¹ for MW-ON and 8 to 24 g C m⁻² year⁻¹ for PWP-ON. See Table 1 for site definitions.

26 years of age. An analysis of specific chronosequences indicates that the burned black spruce (BBS-MB), harvested jack pine (HJP-SK) and harvested Douglas-fir chronosequences (HDF-BC) become C sinks 10, 14 and 18 years after disturbance, respectively, and offset initial C losses caused by the disturbance after 19, 34 and 47 years of regrowth, respectively (Table 3). Giasson et al. (2006) suggested that the speed of post-disturbance recovery is controlled by the speed of GEP recovery against a background level of heterotrophic respiration, which seems to be confirmed by our results (Fig. 1). Using various methods, previous studies of these same forest chronosequences have found that they would become C sinks at ages ranging from 11 to 20 years (Goulden et al., 2011; Grant et al., 2007a,b; Schwalm et al., 2007; Zha et al., 2009). For a set of chronosequences located throughout North America and originating from various disturbance types, Amiro et al. (2010) found that disturbed ecosystems became C sinks at between 10 and 20 years of age. Needle-leaf forests in the U.S have been predicted to become sinks at ages ranging from 4 to 16 years (Thornton et al., 2002), while Kolari et al. (2004) reported that a Scots pine chronosequence transitioned from a source to a sink at 12 years of age.

In comparison to the boreal and coastal forest sites, the afforested white pine plantations (PWP-ON) could be C sources for the first 2 years after planting and could offset initial losses the following year (Table 3). The much shorter time to reach the C compensation point and the higher NEP rates for the

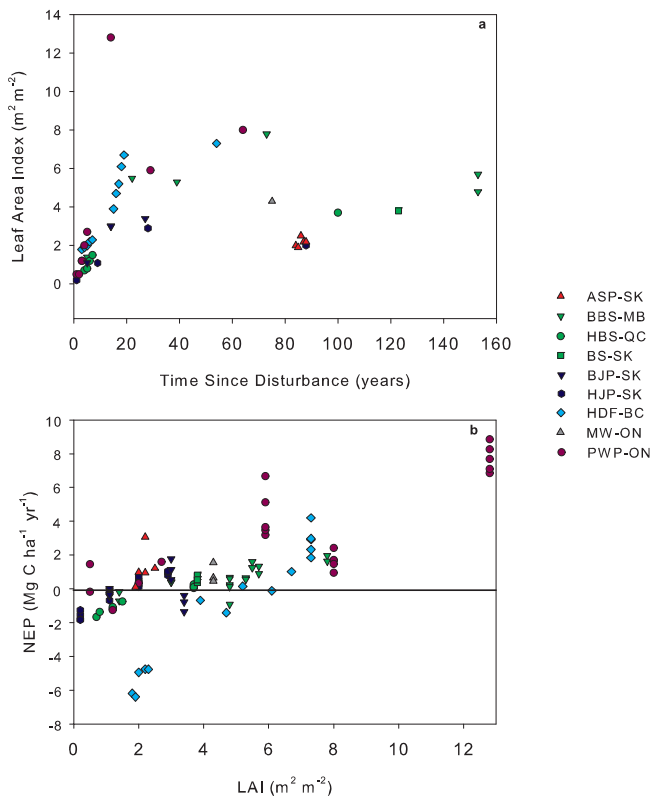


Fig. 2. (a) Leaf area index with respect to time since disturbance. (b) Annual NEP with respect to leaf area index. See Table 1 for site definitions.

PWP-ON chronosequence compared to other chronosequences in this study are likely due to the low residual soil carbon of the abandoned agricultural land on which the PWP-ON chronosequence was established (Peichl et al., 2010a), which would have resulted in significantly lower respiration rates. In particular, this low carbon stock legacy enabled these plantations to become C sinks after only 2 years, in contrast to the very productive Douglas-fir stands which took 18 years to become sinks. Clark et al. (2004) reported similarly high rates of NEP for a chronosequence of slash pine plantations established on previous plantations (with tree stumps present) in Florida, although the youngest stand in the chronosequence was a strong C source.

According to our regression model, the NEP of the HJP-SK chronosequence would peak at $0.98 \pm 0.30 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ in the 38–43 year age range, whereas the NEP of BBS-MB and HDF-BC would peak at 1.49 ± 0.40 and $2.92 \pm 1.0 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ in the age ranges of 53–68 and 46–49 years, respectively (Table 3). The NEP of the afforested WP-ON chronosequence, on the other hand, would peak at rates of $6.94 \pm 0.66 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at 16–18 years of age. Furthermore, peak NEP would coincide with peak leaf area index (Fig. 2). These results are comparable with those of Pregitzer and Euskirchen (2004) who reported that the peak NEP of the boreal forest biome occurred in the age range of 31–120 years and Zha et al. (2009) who found that the HJP-SK chronosequence would reach peak NEP values at 50 years of age. Thornton et al. (2002), on the other hand reported that evergreen needleleaf forests (harvest and burn origin) in the U.S. could reach peak NEP values much earlier (8–19 years of age) and only 2–7 years after becoming sinks.

Our analysis indicates that boreal forest stands lose between 3.7 ± 1.8 and $12.2 \pm 0.8 \text{ Mg C ha}^{-1}$ during their initial stages of growth after harvesting or fire and before switching to C sinks, while the temperate HDF-BC stands lose $60.3 \pm 2.5 \text{ Mg C ha}^{-1}$ (Table 3). Initial losses by the afforested WP-ON stands are only on the order of $2.1 \pm 1.5 \text{ Mg C ha}^{-1}$ for reasons explained above. In

comparison, Thornton et al. (2002) predicted that the evergreen needle leaf forests located in the warmer climates included in their study typically would lose between 14.9 and $30.5 \text{ Mg C ha}^{-1}$, and as much as, 85 Mg C ha^{-1} . It is important to note that our figures do not include the initial C losses due to combustion and wood harvesting which can be quite variable depending on fire intensity and stand density. For instance, it has been estimated that the average amount of carbon lost due to fires in the region containing the BBS-MB chronosequence is $12.4 \text{ Mg C ha}^{-1}$ (Bond-Lamberty et al., 2004), which, according to our analysis, would take an additional 13 years to offset and reduce the net C gain of this chronosequence from $81.3 \pm 3.4 \text{ Mg C ha}^{-1}$ at 80 years of age to $68.9 \text{ Mg C ha}^{-1}$. Canada-wide estimates of C losses from fire combustion are about 8–20 Mg C ha^{-1} (Amiro et al., 2009), depending on ecoregion, so larger combustion losses from some fires would likely take a longer period for NEP recovery.

We estimate that at 80 years of age, forest stands in this study would have net C gains ranging from 38.1 ± 2.1 to $86.3 \pm 12.1 \text{ Mg C ha}^{-1}$ whereas the afforested white pine plantations could have gained as much as $270 \pm 6.5 \text{ Mg C ha}^{-1}$ at the same age (Table 3). Furthermore, annual NEP of mature forest stands at 80 years of age would range from 0.5 ± 0.2 to $2.0 \pm 3.3 \text{ Mg C ha}^{-1}$ and decrease to values ranging from 0.3 ± 0.2 to $1.4 \pm 3.3 \text{ Mg C ha}^{-1}$ (results not shown) at 100 years of age. We recognize that the projections for net C gain at 80 years of age for the HDF-BC and PWP-ON chronosequences may be somewhat uncertain, because of a lack of data points in that age range and beyond. Trofymow et al. (2008) report a total ecosystem C content estimate of 750 Mg C ha^{-1} for an old-growth Douglas-fir landscape, an amount that can only be reached through sustained net C uptake. Schwalm et al. (2007) predicted a net C gain for the HDF-BC chronosequence of $21.0 \text{ Mg C ha}^{-1}$ by 56 years of age, whereas Grant et al. (2007b) used a process model, Ecosys, to estimate an annual NEP of $2\text{--}4 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at 50 years of age for the same chronosequence. For comparison, our model predicts a net C gain of $27.8 \text{ Mg C ha}^{-1}$ at 56 years and an annual NEP of $2.9 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ at 50 years of age for this ecosystem. Furthermore, fertilization of the HDF-BC chronosequence in early 2007 increased the NEP of the DF49-BC and HDF88-BC by 1.68 and $1.82 \text{ Mg C ha}^{-1} \text{ year}^{-1}$, respectively, while the NEP of the youngest site (HDF00-BC) was likely reduced by $0.03 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ for the last year of data in our analysis (Jassal et al., 2010).

3.2. Stand age and the seasonality of carbon fluxes

GEP season lengths (SL_{GEP}), the contiguous period when GEP was at least 15% of the maximum annual rate, varied with respect to age, plant functional type and climate/geographic region (Table 4). Generally, SL_{GEP} of the forested stands increased with stand age. The deciduous OA-SK stand had considerably shorter growing seasons compared to coniferous stands from the same region, while the Douglas-fir stand and white pine plantations located in temperate regions had longer growing seasons than stands of similar age in other regions. However, stand age did not have an effect on the SL_{GEP} of the afforested white pine plantations (Table 4).

For a 1-year long period of measurements in a chronosequence study of burned stands in Alaska, USA, Welp et al. (2006) reported that the onset of the growing season in a 15-year old stand was delayed by 3 weeks compared to an 80-year old stand and the length of the carbon uptake period (CUP) was reduced at 3- and 15-year old stands. Previous studies using some of the same chronosequences included in this analysis have reported that, over a 2- to 3-year period, recently burned and harvested black spruce stands (BS98-MB, HBS00-QC) had shorter growing seasons with later onsets and earlier endings (Bergeron et al., 2008; McMillan et al., 2008) compared to a mature stand, and a seven to 11-year

Table 4
Day of year start and end dates for GEP growing seasons (GS_{GEP}) and GEP growing season lengths (SL_{GEP} : mean daily GEP > 15% of maximum mean daily GEP for the year) for 2003–2007. Data within parentheses are standard deviations for the means of all years.

Site	Age ^a	2003		2004		2005		2006		2007		Mean all years	
		GS_{GEP}	SL_{GEP}	GS_{GEP}	SL_{GEP}	GS_{GEP}	SL_{GEP}	GS_{GEP}	SL_{GEP}	GS_{GEP}	SL_{GEP}	GS_{GEP}	SL_{GEP}
<i>HJP-SK</i>													
OJP-SK	88	111–287	176	111–286	175	103–288	185	99–283	184	107–286	179	106(5)–286(2)	180(5)
HJP75-SK	28	N/A	N/A	N/A to 286	N/A	103–288	185	98–281	183	107–289	182	103(5)–286(4)	183(2)
HJP94-SK	9	109–282	104	136–286	150	103–263	160	N/A	N/A	N/A	N/A	116(18)–279(13)	162(14)
HJP02-SK	1	N/A	N/A	161–260	99	161–302	141	138–274	136	118–274	156	145(21)–278(18)	133(24)
<i>BJP-SK</i>													
OJP-SK	88	111–287	176	111–286	175	103–288	185	99–283	184	107–286	179	106(5)–286(2)	180(5)
F77-SK	26	N/A	N/A	114–285	171	104–289	185	97–281	184	N/A	N/A	105(9)–285(4)	180(8)
F89-SK	14	108–255	147	118–283	165	105–284	179	N/A	N/A	N/A	N/A	110(7)–274(17)	164(16)
F98-SK	5	109–276	167	116–282	166	106–285	179	101 to N/A	N/A	N/A	N/A	108(6)–281(3)	171(7)
<i>HBS-QC</i>													
EOBS-QC	100	N/A to 289	N/A	133–298	165	114–297	183	104–290	186	115–298	183	117(12)–294(4)	179(10)
HBS00-QC	3	132–287	155	136–280	144	119–284	165	121–282	161	122–279	157	126(8)–282(3)	156(8)
<i>BBS-MB</i>													
BS1850-MB	153	107–284	177	133–283	150	102 to N/A	N/A	N/A	N/A	N/A	N/A	114(17)–279(8)	165(14)
BS30-MB	73	107–284	177	133–284	151	121 to N/A	N/A	N/A	N/A	N/A	N/A	120(13)–265(32)	145(35)
BS64-MB	39	108–281	173	135–284	149	106 to N/A	N/A	N/A	N/A	N/A	N/A	116(16)–277(10)	160(12)
BS81-MB	22	121–281	160	138–282	144	122 to N/A	N/A	N/A	N/A	N/A	N/A	127(10)–277(8)	150(9)
BS89-MB	14	122–257	135	145–270	125	132 to N/A	N/A	N/A	N/A	N/A	N/A	133(12)–264(7)	131(5)
BS98-MB	5	144–256	112	160–254	94	148 to N/A	N/A	N/A	N/A	N/A	N/A	151(8)–258(5)	107(11)
<i>HDF-BC</i>													
DF49-BC	54	29–313	284	36–305	269	34–326	292	33–312	279	40–325	285	34(4)–316(9)	282(9)
HDF88-BC	15	42–321	279	54–315	261	30–316	286	17–314	297	49–325	276	38(15)–318(5)	280(13)
HDF00-BC	3	96–299	203	110–278	168	105–270	165	118–275	157	114–286	172	109(9)–212(11)	173(18)
<i>PWP-ON</i>													
WP39-ON	64	98–305	207	96–313	217	94–317	223	88–310	222	84–318	234	92(6)–313(5)	221(10)
WP74-ON ^b	29	99–327	228	85–314	239	95–324	229	85–330	245	83–323	240	89(7)–326(3)	236(7)
WP89-ON ^b	14	97–326	229	91–326	235	101–325	224	85–330	245	86–320	234	92(7)–325(4)	233(8)
WP02-ON ^b	1	82–325	243	84–314	230	84–317	233	83–313	230	83–307	224	83(1)–315(7)	232(7)
<i>Non-Chrono</i>													
SOBS-SK	123	106–286	180	111–286	175	95–276	181	97–280	183	104–289	185	103(7)–283(5)	181(4)
NOBS-MB	153	124–285	161	135–284	149	104–273	169	108–279	171	108–295	187	116(13)–283(8)	167(14)
OA-SK	84	133–265	132	153–263	110	138–262	124	131–263	132	129–258	129	137(10)–262(3)	125(9)
OMW-ON	74	N/A	N/A	118–252	134	102–289	187	105–281	176	N/A	N/A	108(9)–274(20)	166(28)

^a Time since disturbance, approximate age of stand in 2003.

^b Used gapfilled GEP to calculate season start and end dates for WP74-ON, WP89-ON and WP02-ON.

old harvested jack pine stand (HJP94-SK) tended to have a shorter growing season and later onset (Zha et al., 2009) than a mature stand.

The methods used to identify the growing season in these previous studies varied. Consequently, to better determine the influence of disturbance on SL_{GEP} and the timing of the onset and end of the growing season, we analyzed data from the five forest chronosequences in our data set. We did not include the white pine plantation chronosequence in the analysis because its growing season length did not vary with stand age. The oldest stand in each chronosequence was compared to the younger stands in the same chronosequence. The differences in SL_{GEP} and the timing of the onset and end of the growing season between the oldest stand and younger stands in the chronosequence decreased with increasing age of the younger stands and became minimal when stands reached approximately 15–20 years of age (Fig. 3a, b and Table 4). The youngest stand in each chronosequence had GEP growing seasons that were on average between 9 and 58 days shorter, and as much as 109 days shorter for the HDF00-BC site, than the oldest stand in the same chronosequence (Fig. 3a and Table 4). These shorter growing seasons are attributable to either delays in the start of photosynthesis in the spring (Fig. 3b) or an earlier end to the growing season, or both (Table 4), but the effect of age appears to be more pronounced in the spring than in the autumn.

The shorter GEP growing seasons exhibited by the younger disturbed stands likely result from the transition from the evergreen

conifer dominated canopies of older stands to the deciduous and semi-persistent shrubs and herbaceous plants that dominate the canopies of recently disturbed stands (Goulden et al., 2006; Welp et al., 2006). The age at which there are no longer any differences in SL_{GEP} likely indicates the transition back to an evergreen-dominated canopy, which coincides with the switch from C source to C sink for the chronosequences in this study, and very likely, with canopy closure. Using the *Ecosys* model, Grant et al. (2010) reported that pioneer deciduous plant functional types were mostly responsible for GEP during the first 10 years after clearcutting at the HBS-QC, HJP-SK and HDF-BC chronosequences while the dominant coniferous species were mostly responsible for GEP thereafter. The absence of an age effect on SL_{GEP} for the white pine plantation chronosequence (PWP-ON) is probably because of the very different ground cover properties and dynamics of these intensively managed sites.

Differences in annual NEP among stands in the same chronosequence tended to increase as differences in GEP season length increased (Fig. 3c), with annual NEP decreasing by approximately $40 \text{ g C m}^{-2} \text{ year}^{-1}$ with each 10 day decrease in season length for the Douglas-fir chronosequence and $25 \text{ g C m}^{-2} \text{ year}^{-1}$ for the jack pine and black spruce chronosequences. These rates are similar to carbon uptake rates ranging from 2 to $4 \text{ g C m}^{-2} \text{ d}^{-1}$ reported for coniferous forests in Europe and North America (Churkina et al., 2005) and for mature coniferous and deciduous forests in eastern North America (Richardson et al., 2009).

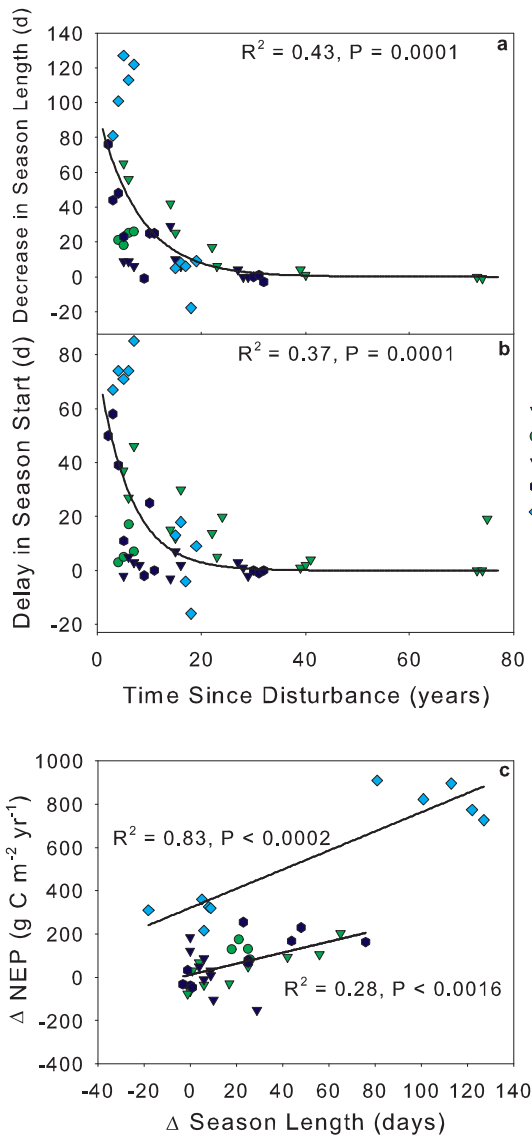


Fig. 3. (a and b) Differences in GEP season length and number of days to the start of GEP growing season, respectively, between the oldest stand in the chronosequence and each of the younger stands in the same chronosequence. The x-axis indicates the age of the younger stand of the pair. (c) Differences in annual NEP between the oldest stand in the chronosequence and each of the younger stands in the same chronosequence, with respect to the difference in season length for the same pair. The afforested white pine plantation chronosequence (PWP-ON) was not included in the analysis because we did not detect an effect of stand age on season length. See Table 1 for site definitions.

The carbon balance of northern ecosystems is sensitive to changes in the timing of spring and autumn (Goulden et al., 1998; Piao et al., 2008; Randerson et al., 1999). Atmospheric CO₂ measurements have shown that warmer and wetter springs are associated with greater ecosystem CO₂ uptake in boreal North America (Goetz et al., 2007; Randerson et al., 1999). Furthermore, satellite-based analyses have examined the effects of increasing temperatures in northern latitudes on vegetation structure and phenology with, at times, conflicting results (Goetz et al., 2005; Myneni et al., 1997; Wang et al., 2011; Zhang et al., 2007). Our results suggest that the influence of stand age on the timing of ecosystem fluxes is continental in scope and needs to be considered when predicting the C balance of forests. This is supported by results from Welp et al. (2006) who reported an increase in the seasonal amplitude of CO₂ over a 15-year old burned stand compared to an 80-year old

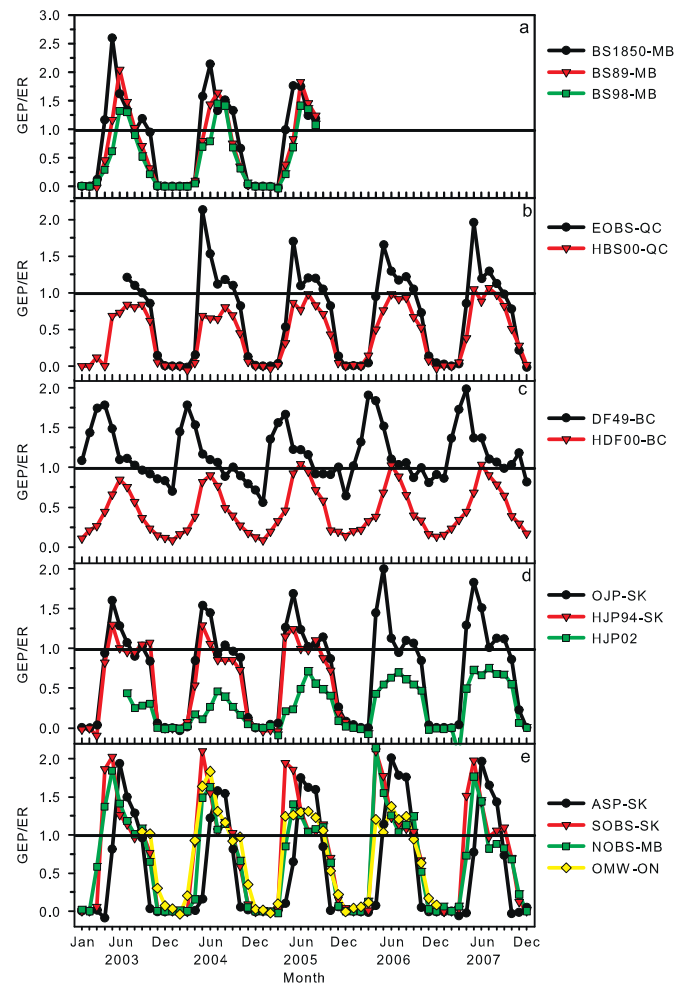


Fig. 4. Monthly GEP/ER for the (a) BBS-MB, (b) HBS-QC (c) HDF-BC, (d) HJP-SK forest chronosequences and the (e) ASP-SK, SOBS-SK, NOBS-MB and MW-ON stands. To simplify the graphical representation, only the oldest stand and the young disturbed stands of each chronosequence are presented in (a), (b), (c), and (d). See Table 1 for site definitions.

stand, along with a delayed onset of the growing season. Furthermore, Zimov et al. (1999) reported that disturbed Siberian forest stands had greater seasonal amplitudes of CO₂ compared to undisturbed forest stands, these greater amplitudes being accompanied by shorter CUPs, and these differences among stands were linked to shifts from coniferous species to grasses, herbs and deciduous species.

With the exception of the burned jack pine (BJP-SK) and plantation white pine chronosequences (PWP-ON), the delay in the springtime start of the GEP growing season for the youngest stands leads them to reach maximum monthly GEP/ER ratios 1–3 months later compared to older stands (Fig. 4a–d). The mature deciduous aspen stand (ASP-SK) showed a similar pattern, where GEP/ER ratios peaked in June or July, 1–2 months after the mature coniferous stands (Fig. 4e). These results indicate that recently harvested stands can only attain maximum sink or minimum source strength once their deciduous dominated canopy is fully developed.

3.3. Controls of annual GEP, NEP and ER

Given the strong relationship between C fluxes and stand age, stands were divided into three age classes according to time since disturbance/age (mature: 73–153 years, intermediate-aged: 23–64 years and young: 1–15 years) to identify the

Table 5
Significant results from a forward stepwise regression analysis of annual GEP, ER and NEP regressed on selected meteorological and structural variables for mature (73–153 years), intermediate-aged (22–64 years) and young recently disturbed (1–15 years) age classes. Only independent variables retained in the model ($p=0.05$ for entry) are presented.

Dependant variable	Independent variable ^a	Partial $R^{2†}$	$R^{2§}$	p
Annual GEP – mature ^b	SWC-GS	0.50	0.85	<0.0001
	T_s -GS	0.35		
Annual ER – mature ^b	T_s	0.44	0.86	<0.0001
	SWC-GS	0.42		
Annual NEP – mature ^b	T_a -GS	0.44	0.44	0.0003
Annual GEP – intermediate ^c	SL _{GEP}	0.91	0.95	<0.0001
	SWC-GS	0.04		
Annual ER – intermediate ^c	SL _{GEP}	0.89	0.94	<0.0001
	SWC-GS	0.05		
Annual NEP – intermediate ^c	T_{s0}	0.61	0.74	<0.0001
	T_s	0.12		
Annual GEP – young ^d	LAI	0.87	0.90	<0.0001
	SL _{GEP}	0.03		
Annual ER – young ^d	SNOW	0.70	0.90	<0.0001
	LAI	0.13		
	T_s	0.05		
	T_a	0.02		
Annual NEP – young ^d	ns ^e	ns	ns	ns

^a Independent variables are listed in the order they were introduced into the model (the variable having the most influence first). SWC-GS: growing season soil water content, T_s -GS: growing season mean near surface soil temperature, T_s : annual mean near surface soil temperature, T_a -GS: growing season mean air temperature, SL_{GEP}: photosynthetic growing season length, T_{s0} : number of days when near surface soil temperature <0 °C, LAI: leaf area index, SNOW: number of days with snow cover, T_a : mean annual air temperature.

^b BS1850-MB not included in analysis because at least one meteorological variable was not available.

^c WP74-ON not included in analysis because at least one meteorological variable was not available.

^d WP89-ON not included in analysis because at least one meteorological variable was not available.

^e No significant variables.

[†] Coefficient of partial determination for each significant independent variable.

[§] Coefficient of determination for the final model.

meteorological and/or structural variables having the most significant effects on annual GEP, ER and NEP. A stepwise regression analysis indicated that the combination of mean growing season volumetric soil water content (SWC-GS) and near-surface soil temperature (T_s) explained 85% and 86% of the variability in annual GEP and ER, respectively, of mature stands, and growing season mean air temperature explained 44% of the variation in annual NEP (Table 5). Total above-ground biomass of mature stands was also strongly and positively correlated to all three C fluxes (Tables 5 and 6).

Interestingly, SL_{GEP} of mature stands was strongly and negatively correlated to annual GEP and ER (Table 6). Although negative correlations between growing season length and NEP have been reported for sub-alpine forests and linked to decreased water availability due to an earlier snow-melt (Hu et al., 2010; Sacks et al., 2007), we believe the negative correlations we found between SL_{GEP} and GEP and ER were caused by the presence of different plant functional types in the analysis of mature stands. The mature deciduous aspen (ASP-SK) and mixedwood (MW-ON) stands tended to have higher annual GEP and ER rates (Fig. 1b) and shorter growing seasons (Table 4) compared to the boreal mature stands.

Previous multi-site regional and global analyses of climatic controls on C fluxes have yielded somewhat similar results to those we found for mature boreal stands in Canada. Using global datasets, Luysaert et al. (2007) reported that 71% of the variability in annual GEP was explained by air temperature and precipitation, whereas Law et al. (2002) reported that 64% of the variation in GEP was explained by air temperature and site water balance. Janssens et al. (2001) and Law et al. (2002) both found poor correlations between annual ER and mean annual air temperatures. Reichstein et al. (2007), on the other hand, reported that annual ER and GEP of European sites located above 52°N were correlated with mean annual

air temperature and sites located below 52°N were correlated with available soil moisture. Finally, annual NEP has been reported by Yi et al. (2010) to be strongly correlated with mean annual air temperature at mid- and high-latitude sites, whereas Law et al. (2002) and Piao et al. (2008) reported only weak correlations between annual NEP and water balance (Law et al., 2002) and mean annual air temperature.

The regression and correlation analyses indicate that annual C fluxes of the intermediate-aged sites are related to both climate and stand structure. SL_{GEP} (partial $R^2 = 0.91$ and 0.89) combined with SWC-GS explained 95% and 94% of the variation in the annual GEP and ER of these stands, while 74% of annual NEP was explained by a combination of the number of days the soil was frozen (T_{s0}) and T_s (Table 5). LAI and total rainfall during the GEP growing season (RAIN-GS) were also strongly correlated to annual GEP of the intermediate-aged stands while LAI, temperature (soil and/or air), snow cover and rainfall (ER only) were also strongly correlated to annual ER and NEP (Table 6). We believe that the strong correlation between LAI and the C fluxes actually reflect regional climate differences among the stands within the intermediate-aged group. The DF49-BC and WP39-ON located in temperate regions had larger fluxes (Fig. 1) and greater LAI (Fig. 2a) compared to the other stands in this age class and LAI was also strongly correlated to both annual soil and air temperatures ($r = 0.81$ and 0.78 , respectively, results not shown). This would indicate that, as with mature stands, the fluxes of the intermediate-aged stands in this study are mainly affected by climate through SL_{GEP} and air and soil temperatures.

Our results indicate that the combination of LAI (partial $R^2 = 0.87$) and SL_{GEP} explained 90% of the variability in the annual GEP of young, recently disturbed stands (Table 5). The very strong positive correlation between LAI and GEP confirms that stand

Table 6
Pearson correlation coefficients (r , first line) and probabilities (p , second line) for correlations calculated between annual GEP, ER and NEP between mature (73–153 years), intermediate-aged (22–64 years), and young recently disturbed (1–15 years) age classes and selected environmental and site variables.

	T_a^a	T_s	T_a -GS	T_s -GS	T_{s0}	SNOW	RAIN-GS	SWC-GS	PPFD-GS	SL _{GEP}	AGB	LAI
Annual GEP – mature ^d	n/a ^b	n/a	0.4996 0.0110	0.6152 0.0011	n/a	n/a	ns ^c	0.7067 <0.0001	0.6397 0.0006	–0.5524 0.0042	0.7036 <0.0001	ns
Annual ER – mature ^d	0.5412 0.0052	0.6667 0.0003	n/a	n/a	–0.4409 0.0274	–0.4262 0.0336	ns	0.6506 0.0004	n/a	–0.4692 0.0180	0.5606 <0.0001	–0.4127 0.0403
Annual NEP – mature ^d	ns	ns	0.6646 0.0003	0.4740 0.0167	ns	ns	–0.4632 0.0197	ns	ns	ns	0.5889 <0.0020	ns
Annual GEP – intermediate ^e	n/a	n/a	ns	ns	n/a	n/a	0.6736 0.0022	ns	ns	0.9562 <0.0001	n/a	0.6730 0.0022
Annual ER – intermediate ^e	0.7419 0.0007	0.6797 0.0027	n/a	n/a	–0.8583 <0.0001	–0.7039 0.0016	0.6742 0.0030	ns	n/a	0.9447 <0.0001	n/a	0.6502 0.0047
Annual NEP – intermediate ^e	0.6484 0.0049	ns	ns	ns	–0.7851 0.0002	–0.7100 0.0014	ns	ns	ns	0.7604 0.0004	n/a	0.6466 0.0050
Annual GEP – young ^f	n/a	n/a	ns	ns	n/a	n/a	0.5207 0.0016	ns	ns	0.7467 <0.0001	n/a	0.9321 <0.0001
Annual ER – young ^f	0.7149 <0.0001	0.3735 0.0323	n/a	n/a	–0.6609 <0.0001	–0.8344 <0.0001	0.3848 0.0270	ns	n/a	0.6286 <0.0001	n/a	0.7972 <0.0001
Annual NEP – young ^f	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	n/a	ns

^a T_a : mean annual air temperature; T_s : mean annual near-surface soil temperature; T_a -GS: mean GEP growing season air temperature; T_s -GS: mean GEP growing season near surface soil temperature; T_{s0} : number of days when $T_s < 0^\circ\text{C}$ on annual basis; SNOW: number of days with snow cover on annual basis; RAIN-GS: total growing season rainfall; SWC-GS: mean growing season soil water content; PPFD-GS: growing season mean PPFD; SL_{GEP}: GEP growing season length; AGB: total above-ground biomass; LAI: leaf area index.

^b n/a: r not calculated for the pair of variables, no r was calculated between AGB and carbon fluxes of intermediate-aged and young recently disturbed stands because there was only a one-time AGB measurement available for each stand and AGB varies as stands age to maturity.

^c ns: r not significant at the 0.05 level.

^d BS1850-MB not included in analysis because at least one meteorological variable was not available.

^e WP74-ON not included in analysis because at least one meteorological variable was not available.

^f WP89-ON not included in analysis because at least one meteorological variable was not available.

structure is more important than climate in determining GEP fluxes of young stands in the years immediately following a disturbance. Annual ER, on the other hand, was correlated with both climate and stand structure, with the length of the snow-cover period, LAI and soil and air temperatures combining to explain 90% of the variation in ER from these stands (Table 5). No significant regressions or correlations were found for annual NEP of the young stands which is a similar result to Law et al. (2002) and Piao et al. (2008), who found only weak correlations between annual NEP and mean annual air temperature.

4. Conclusion

Coordinated measurements of ecosystem fluxes are important for understanding the influence of disturbance and climate variability on the C cycle of Canadian forests at the continental scale. Our results have shown that, depending on species/ecosystem type, harvested and burned forest stands are sources of carbon for the first 9–17 years following the disturbance and may lose between $3.7 \pm 1.8 \text{ Mg C ha}^{-1}$ and $60.3 \pm 2.5 \text{ Mg C ha}^{-1}$ during this period. These initial losses would be offset when the stands had reached 19–47 years of age (excluding the initial C lost through either combustion or harvest removals) and stands would attain peak NEP values of 0.89 ± 0.19 – $2.92 \pm 1.0 \text{ Mg C ha}^{-1}$ at ages ranging from 35 to 55 years. We also estimate that forest stands in Canada achieve net total gains of 38–86 Mg C ha^{-1} at 80 years of age and are carbon neutral or weak sinks at 100 years of age. Forest plantations established on abandoned agricultural land in the temperate zone, on the other hand, only lose $2.1 \pm 1.5 \text{ Mg C ha}^{-1}$ over the initial few years following establishment and then become a C sink. Overall, these data should help to more accurately determine the influences of forest management on the Canadian C budget by serving as data benchmarks for C cycle models.

There is little information currently available in the literature concerning the effects of disturbance on the onset, end, and duration of the growing season. Our results indicate that, with the exception of the afforested plantation stands, the youngest stands in each chronosequence had GEP growing seasons that were between 9 and 109 days shorter than the oldest stand in the same chronosequence. The differences in GEP season length decreased with increasing stand age, becoming minimal at 15–20 years of age and coinciding with the transition from C source to sink. The shorter growing seasons of the younger stands were associated with changes in the seasonal pattern of the C fluxes. Thus, disturbance influences not only stand structure and species composition, but also the seasonality of the GEP and NEP fluxes. Atmospheric CO_2 concentrations in the northern hemisphere also have a very strong seasonality that has a large influence on global patterns of atmospheric CO_2 . The changes in the seasonality of ecosystem fluxes following disturbance across the range of ecosystems described in this study improve our understanding of how ecological disturbance might influence the time series of atmospheric CO_2 concentrations. This could be important for separating the influences of climate variability versus disturbance at larger spatial scales.

Our results indicate that climate (soil moisture, air and soil temperatures and growing season length) is the primary factor affecting annual GEP, ER and NEP of mature stands and stand structure, through LAI, is the main factor affecting the annual GEP of young, recently disturbed stands. These differences in C flux drivers need to be considered when we try to detect a climate change signal that is mixed into a disturbance signal. While annual ER of young, recently disturbed stands is correlated with both climate and LAI, none of the variables tested were found to be related to annual NEP of these stands.

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References

- Amiro, B.D., 2010. Estimating annual carbon dioxide eddy fluxes using open-path analysers for cold forest sites. *Agric. For. Meteorol.* 150, 366–1372.
- Amiro, B.D., Barr, A.G., Barr, J.G., Black, T.A., Bracho, R., Brown, M., Chen, J., Clark, K.L., Davis, K.J., Desai, A.R., Dore, S., Engel, V., Fuentes, J.D., Goldstein, A.H., Goulden, M.L., Kolb, T.E., Lavigne, M.B., Law, B.E., Margolis, H.A., Martin, T., McCaughey, J.H., Misson, L., Montes-Helu, M., Noormets, A., Randerson, J.T., Starr, G., Xiao, J., 2010. Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *J. Geophys. Res.* 115, G00K02, <http://dx.doi.org/10.1029/2010JG001390>.
- Amiro, B.D., Barr, A.G., Black, T.A., Iwashita, H., Kljun, N., McCaughey, J.H., Morgenstern, K., Murayama, S., Nesic, Z., Orchansky, A.L., Saigusa, N., 2006. Carbon, energy and water fluxes at mature and disturbed forest sites, Saskatchewan, Canada. *Agric. For. Meteorol.* 136, 237–251.
- Amiro, B.D., Cantin, A., Flannigan, M.D., de Groot, W.J., 2009. Future emissions from Canadian boreal forest fires. *Can. J. For. Res.* 39, 383–395.
- Arain, M.A., Restrepo-Coupe, N., 2005. Net ecosystem production in a temperate pine plantation in southeastern Canada. *Agric. For. Meteorol.* 128, 223–241.
- Aubinet, M., Grelle, A., Ibrom, A., et al., 2000. Estimates of the annual net carbon and water exchange of forests: the EUROFLUX methodology. *Adv. Ecol. Res.* 30, 113–175.
- Baldocchi, D., 2008. 'Breathing' of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. *Aust. J. Bot.* 56 (1), 26.
- Barr, A.G., Black, T.A., Hogg, E.H., Kljun, N., Morgenstern, K., Nesic, Z., 2004. Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. *Agric. For. Meteorol.* 126, 237–255.
- Bergeron, O., Margolis, H.A., Coursolle, C., Giasson, M.-A., 2008. How does forest harvest influence carbon dioxide fluxes of black spruce ecosystems in eastern North America. *Agric. For. Meteorol.* 148, 537–548.
- Bond-Lamberty, B., Wang, C., Gower, S.T., 2004. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. *Global Change Biol.* 10, 473–487.
- Burba, G.G., McDermitt, D.K., Grelle, A., Anderson, D.J., Xu, L.K., 2008. Addressing the influence of instrument surface heat exchange on the measurements of CO_2 flux from open-path analyzers. *Global Change Biol.* 14, 1854–1876.
- Canadell, J.G., Raupach, M.R., 2008. Managing forests for climate change mitigation. *Science* 320, 1456–1457.
- Canadell, J.G., Pataki, D.E., Gifford, R., Houghton, R.A., Luo, Y., Raupach, M.R., Smith, P., Steffen, W., 2007a. Saturation of the terrestrial carbon sink. In: Canadell, J.G., Pataki, D.E., Pitteka, L.F. (Eds.), *Terrestrial Ecosystems in a Changing World*. Springer-Verlag, Berlin, pp. 59–74.
- Canadell, J.G., Le Quere, C., Raupach, M.R., Field, C.B., Buitenhuis, E.T., Ciais, P., Conway, T.J., Gillett, N.P., Houghton, R.A., Marland, G., 2007b. Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proc. Natl. Acad. Sci. U. S. A.* 104, 18866–18870.
- Churkina, G., Schimel, D., Braswell, B.H., Xiao, X., 2005. Spatial analysis of growing season length control over net ecosystem exchange. *Global Change Biol.* 11, 1777–1787.
- Ciais, P., Canadell, J.G., Luysaert, S., Chevallier, F., Shvidenko, A., Poussi, Z., Jonas, M., Peylin, P., King, A.W., Schulze, E.-D., Piao, S., Rödenbeck, C., Peters, W., Bréon, F.M., 2010. Can we reconcile atmospheric estimates of the northern terrestrial carbon sink with land-based accounting? *Curr. Opin. Environ. Sustain.* 2, 1–6.
- Clark, K.L., Gholz, H.L., Castro, M.S., 2004. Carbon dynamics along a chronosequence of slash pine plantations in North Florida. *Ecol. Appl.* 14, 1154–1171.
- Coursolle, C., Margolis, H.A., Barr, A.G., Black, T.A., Amiro, B.D., McCaughey, J.H., Flanagan, L.B., Lafleur, P.M., Roulet, N.T., Bourque, C.P.-A., Arain, M.A., Wofsy, S.C., Dunn, A., Morgenstern, K., Orchansky, A.L., Bernier, P.-Y., Chen, J.M., Kidston, J., Saigusa, N., Hedstrom, N., 2006. Late-summer carbon fluxes from Canadian forests and peatlands along an east-west continental transect. *Can. J. For. Res.* 36, 783–800.

- Dragoni, D., Schmid, H.P., Grimmond, C.S.B., Loescher, H.W., 2007. Uncertainty of annual net ecosystem productivity estimated using eddy covariance flux measurements. *J. Geophys. Res.* 112 (1), 9.
- Dunn, A.L., Barford, C.C., Wofsy, S.C., Goulden, M.L., Daube, B.C., 2007. A long-term record of carbon exchange in a boreal black spruce forest: means, response to interannual variability, and decadal trends. *Global Change Biol.* 13, 577–590.
- Giasson, M.-A., Coursolle, C., Margolis, H.A., 2006. Ecosystem-level CO₂ fluxes from a boreal cutover in eastern Canada before and after scarification. *Agric. For. Meteorol.* 140, 23–40.
- Goetz, S.J., Mack, M.C., Gurney, K.R., Randerson, J.T., Houghton, R.A., 2007. Ecosystem responses to recent climate change and fire disturbance at northern high latitudes: observations and model results contrasting northern Eurasia and North America. *Environ. Res. Lett.* 2, <http://dx.doi.org/10.1088/1748-9326/2/4/045031>.
- Goetz, S.J., Bunn, A.G., Fiske, G.J., Houghton, R.A., 2005. Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proc. Nat. Acad. Sci. U. S. A.* 102, 13521–13525.
- Goulden, M.L., McMillan, M.S., Winston, G.C., Rocha, A.V., Manies, K.L., Harden, J.W., Bond-Lamberty, B.P., 2011. Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biol.* 17, 855–871, <http://dx.doi.org/10.1111/j.1365-2486.2010.02274.x>.
- Goulden, M.L., Winston, G.C., McMillan, A.M.S., Litvak, M.E., Read, E.L., Rocha, A.V., Elliot, J.R., 2006. An eddy covariance mesonet to measure the effect of forest age on land-atmosphere exchange. *Global Change Biol.* 12, 2146–2162.
- Goulden, M.L., Wofsy, S.C., Harden, J.W., Trumbore, S.E., Crill, P.M., Gower, S.T., Fries, T., Daube, B.C., Fan, S.-M., Sutton, D.J., Bazzaz, A., Munger, J.W., 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* 279, 214–217, <http://dx.doi.org/10.1126/science.279.5348.214>.
- Grant, R.F., Barr, A.G., Black, T.A., Gaumont-Guay, D., Iwashita, H., Kidson, J., McCaughey, H., Morgenstern, K., Murauama, S., Nesic, Z., Saigusa, N., Shashkov, A., Zha, T., 2007a. Net ecosystem productivity of boreal jack pine stands regenerating from clearcutting under current and future climates. *Global Change Biol.* 13, 1423–1440.
- Grant, R.F., Barr, A.G., Black, T.A., Margolis, H.A., McCaughey, J.H., Trofymow, J.A., 2010. Net ecosystem productivity of temperate and boreal forests after clearcutting – a Fluxnet-Canada measurement and modelling synthesis. *Tellus* 62B, 475–496.
- Grant, R.F., Black, T.A., Humphreys, E.R., Morgenstern, K., 2007b. Changes in net ecosystem productivity with forest age following clearcutting of a coastal Douglas-fir forest: testing a mathematical model with eddy covariance measurements along a forest chronosequence. *Tree Physiol.* 27, 115–131.
- Hu, J., Moore, D.J.P., Burns, S.P., Monson, R.K., 2010. Longer growing seasons lead to less carbon sequestration by a subalpine forest. *Global Change Biol.* 16, 771–783.
- Humphreys, E.R., Black, T.A., Morgenstern, K., Cai, T., Drewitt, G.B., Nesic, Z., Trofymow, J.A., 2006. Carbon dioxide fluxes in coastal Douglas-fir stands at different stages of development after clearcut harvesting. *Agric. For. Meteorol.* 140, 6–22.
- Janssens, A., Lankreijer, H., Matteucci, G., et al., 2001. Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biol.* 7, 269–278.
- Jassal, R.S., Black, T.A., Cai, T., Ethier, G., Pepin, S., Brümmer, C., Nesic, Z., Spittlehouse, D.L., Trofymow, J.A., 2010. Impact of nitrogen fertilization on carbon and water balances in a chronosequence of three Douglas-fir stands in the Pacific Northwest. *Agric. For. Meteorol.* 150, 208–218.
- Kolari, P., Pumpanen, J., Rannik, U., Ilvesniemi, H., Hari, P., Berninger, F., 2004. Carbon balance of different aged Scots pine forests in Southern Finland. *Global Change Biol.* 10, 1106–1119.
- Krishnan, P., Black, T.A., Barr, A.G., Grant, N.J., Gaumont-Guay, D., Nesic, Z., 2008. Factors controlling the interannual variability in the carbon balance of a southern boreal spruce forest. *J. Geophys. Res.* 113, D09109, <http://dx.doi.org/10.1029/2007JD008965>.
- Krishnan, P., Black, T.A., Grant, N.J., Barr, A.G., Hogg, E.H., Jassal, R.S., Morgenstern, K., 2006. Impact of changing soil moisture on net ecosystem productivity of a boreal aspen forest during and following drought. *Agric. For. Meteorol.* 139, 208–223.
- Kurz, W.A., Dymond, C.C., Stinson, G., Rampley, G.J., Neilson, E.T., Carroll, A.L., Ebata, T., Safranyik, L., 2008a. Mountain pine beetle and forest carbon feedback to climate change. *Nature* 452, 987–990.
- Kurz, W.A., Stinson, G., Rampley, G., 2008b. Could increased boreal forest ecosystem productivity offset carbon losses from increased disturbances? *Philos. Trans. R. Soc. Lond. Ser. B* 363, 2261–2269, <http://dx.doi.org/10.1098/rstb.2007.2198>.
- Kurz, W.A., Stinson, G., Rampley, G.J., Dymond, C.C., Neilson, E.T., 2008c. Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. *Proc. Natl. Acad. Sci. U.S.A.* 105, 1551–1555.
- Kurz, W.A., Apps, M.J., 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. *Ecol. Appl.* 9, 526–547.
- Kurz, W.A., Apps, M.J., 1995. An analysis of future carbon budgets of Canadian boreal forests. *Water Air Soil Pollut.* 82, 321–331.
- Law, B.E., Falge, E., Gu, L., et al., 2002. Environmental controls over carbon dioxide and water vapor exchange of terrestrial vegetation. *Agric. For. Meteorol.* 113, 97–120.
- Le Quéré, C., Raupach, M.R., Canadell, J.G., Marland, G., et al., 2009. Trends in the sources and sinks of carbon dioxide. *Nat. Geosci.* 2, 831–836, <http://dx.doi.org/10.1038/ngeo689>.
- Le Quéré, C., Rödenbeck, C., Buitenhuis, E.T., Conway, T.J., Langenfelds, R., Gomez, A., Labuschagne, C., Ramonet, M., Nakazawa, T., Metz, N., Gillett, N., Heimann, M., 2007. Saturation of the southern ocean CO₂ sink due to recent climate change. *Science* 316, 1735–1738.
- Luyssaert, S., Inglima, I., Jung, M., et al., 2007. CO₂ balance of boreal, temperate, and tropical forests derived from a global database. *Global Change Biol.* 13, 1–29.
- Margolis, H.A., Flanagan, L.B., Amiro, B.D., 2006. The Fluxnet-Canada Research Network: influence of climate and disturbance on carbon cycling in forest and peatlands. *Agric. For. Meteorol.* 140, 1–5, <http://dx.doi.org/10.1016/j.agrformet.2006.08.013>.
- McCaughey, J.H., Pejam, M.R., Arain, M.A., Cameron, D.A., 2006. Carbon dioxide and energy fluxes from a boreal mixedwood forest ecosystem in Ontario, Canada. *Agric. For. Meteorol.* 140, 79–96.
- McMillan, A.M.S., Winston, G.C., Goulden, M.L., 2008. Age-dependent response of boreal forest to temperature and rainfall variability. *Global Change Biol.* 14, 1904–1916.
- Mkhabela, M.S., Amiro, B.D., Barr, A.G., Black, T.A., Hawthorne, I., Kidston, J., McCaughey, J.H., Orchansky, A.L., Nesic, Z., Sass, A., Shashkov, A., Zha, T., 2009. Comparison of carbon dynamics and water use efficiency following fire and harvesting in Canadian boreal forests. *Agric. For. Meteorol.* 149, 783–794.
- Morgenstern, K., Black, T.A., Humphreys, E.R., Griffis, T.J., Drewitt, G.B., Cai, T., Nesic, Z., Spittlehouse, D.L., Livingston, N.J., 2004. Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas-fir forest during an El Niño/La Niña cycle. *Agric. For. Meteorol.* 123, 201–219.
- Myneni, R.B., Keeling, C.D., Nemani, R.R., 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386, 698–701.
- Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests, 1990–2007. *Science*, 10.1126/science.1201609.
- Peichl, M., Arain, M.A., 2006. Above- and belowground ecosystem biomass and carbon pools in an age-sequence of temperate pine plantation forests. *Agric. For. Meteorol.* 140, 51–63.
- Peichl, M., Arain, M.A., Brodeur, J.J., 2010a. Age effects on carbon fluxes in temperate pine forests. *Agric. For. Meteorol.* 150, 1090–1101, <http://dx.doi.org/10.1016/j.agrformet.2010.04.008>.
- Peichl, M., Brodeur, J.J., Khomik, M., Arain, M.A., 2010b. Biometric and eddy-covariance based estimates of carbon fluxes in an age-sequence of temperate pine forests. *Agric. For. Meteorol.* 150, 952–965, <http://dx.doi.org/10.1016/j.agrformet.2010.03.002>.
- Piao, S., Ciais, P., Friedlingstein, P., Peylin, P., Reichstein, M., Luyssaert, S., Margolis, H., Fang, J., Barr, A., Chen, A., Grelle, A., Hollinger, D., Laurila, T., Lindroth, A., Richardson, A., Vesala, T., 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature* 451, 49–53.
- Pregitzer, K.S., Euskirchen, E.S., 2004. Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biol.* 10, 2052–2077.
- Randerson, J.T., Field, C.B., Fung, I.Y., Tans, P.P., 1999. Increases in early season net ecosystem uptake explain changes in the seasonal cycle of atmospheric CO₂ at high northern latitudes. *Geophys. Res. Lett.* 26, 2765–2768.
- Reichstein, M., Papale, D., Valentini, R., Aubinet, M., Bernhofer, C., Knohl, A., Laurila, T., Lindroth, A., Moors, E., Pilegaard, K., Seufert, G., 2007. Determinants of terrestrial ecosystem carbon balance inferred from European eddy covariance flux sites. *Geophys. Res. Lett.* 34, L01402, <http://dx.doi.org/10.1029/2006GL027880>.
- Richardson, A.D., Hollinger, D.Y., Dail, D.B., Lee, J.T., Munger, J.W., O'Keefe, J., 2009. Influence of spring phenology on seasonal and annual carbon balance in two contrasting New England forests. *Tree Physiol.* 29, 321–331.
- Rödenbeck, C., Houweling, S., Gloor, M., Heimann, M., 2003. CO₂ flux history 1982–2001 inferred from atmospheric data using a global inversion of atmospheric transport. *Atmos. Chem. Phys.* 3, 1919–1964.
- Sacks, W.J., Schimel, D.S., Monson, R.K., 2007. Coupling between carbon cycling and climate in a high elevation, subalpine forest: a model-data fusion analysis. *Oecologia* 151, 54–68.
- Sarmiento, J.L., Gruber, N., 2002. Sinks for anthropogenic carbon. *Phys. Today* 55, 30–36.
- Sellers, P.K., Hall, F.G., Kelly, R.D., Black, A., Baldocchi, D., Berry, J., Ryan, M., Ranson, K.J., Crill, P.M., Lettenmaier, P., Margolis, H., Cihlar, J., Newcomer, J., Fitzjarrald, D., Jarvis, P.G., Gower, S.T., Halliwell, D., Williams, D., Godison, B., Wickland, D.E., Guertin, F.E., 1997. BOREAS in 1997: experiment overview, scientific results, and future directions. *J. Geophys. Res.* 102, 28, 731–28,769.
- Schwalm, C.R., Black, T.A., Morgenstern, K., Humphreys, E.R., 2007. A method for deriving net primary productivity and component respiratory fluxes from tower-based eddy covariance data: a case study using a 17-year data record from a Douglas-fir chronosequence. *Global Change Biol.* 13, 370–385.
- Stephens, B.B., Gurney, K.R., Tans, P.P., Sweeney, C., Peters, W., Bruhwiler, L., Ciais, P., Ramonet, M., Bousquet, P., Nakazawa, T., Aoki, S., Machida, T., Inoue, G., Vinichenko, N., Lloyd, J., Jordan, A., Heimann, M., Shibistova, O., Langenfelds, R.L., Steele, L.P., Francey, R.J., Denning, A.S., 2007. Weak northern and strong tropical land carbon uptake from vertical profiles of atmospheric CO₂. *Science* 316, 1732–1735.
- Tans, P.P., Fung, I.Y., Taikahashi, T., 1990. Observational constraints on the global atmospheric CO₂ budget. *Science* 247, 1431–1438.
- Tarnocai, C., Canadell, J.G., Schuur, E.A.G., Kuhry, P., Mazhitova, G., Zimov, S., 2009. Soil organic carbon pools in the northern circumpolar permafrost region. *Global Biogeochem. Cycles* 23, GB2023, <http://dx.doi.org/10.1029/2008GB003327>.
- Thornton, P.E., Law, B.E., Gholz, H.L., Clark, K.L., Falge, E., Ellsworth, D.S., Goldstein, A.H., Monson, R.K., Hollinger, D., Falk, M., Chen, J., Sparks, J.P., 2002.

- Modelling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agric. For. Meteorol.* 113, 185–222.
- Trofymow, J.A., Stinson, G., Kurz, W.A., 2008. Derivation of a spatially explicit 86-year retrospective carbon budget for a landscape undergoing conversion from old-growth to managed forests on Vancouver Island, BC. *For. Ecol. Manage.* 256, 1677–1691.
- Wang, X., Piao, S., Ciais, P., Li, J., Friedlingstein, P., Koven, C., Chen, A., 2011. Spring temperature change and its implication in the change of vegetation growth in North America from 1982 to 2006. *Proc. Nat. Acad. Sci. U. S. A.* 108, 1240–1245.
- Welp, L.R., Randerson, J.T., Liu, H.P., 2006. Seasonal exchange of CO₂ and δ¹⁸O-CO₂ varies with postfire succession in boreal forest ecosystems. *J. Geophys. Res.* 111, G03007, <http://dx.doi.org/10.1029/2005JG000126>.
- Yi, C., Ricciuto, D., Li, R., et al., 2010. Climate control of terrestrial carbon exchange across biomes and continents. *Environ. Res. Lett.* 5, <http://dx.doi.org/10.1088/1748-9326/5/3/034007>.
- Zha, T., Barr, A.G., Black, T.A., McCaughey, J.H., Bhatti, J., Hawthorne, I., Krishnan, P., Kidston, J., Saigusa, N., Shashkov, A., Nesic, Z., 2009. Carbon sequestration in boreal jack pine stands following harvesting. *Global Change Biol.* 15, 1475–1487.
- Zhang, K., Kimball, J.S., Zhao, M.S., Oechel, W.C., Cassano, J., Running, S.W., 2007. Sensitivity of pan-Arctic terrestrial net primary productivity simulations to daily surface meteorology from NCEP-NCAR and ERA-40 reanalyses. *J. Geophys. Res. Biogeosci.* 112, G0101.
- Zimov, S.A., Davidov, S.P., Zimova, G.M., Davidova, A.I., Chapin III, F.S., Chapin, M.C., Reynolds, J.F., 1999. Contribution of disturbance to increasing seasonal amplitude of atmospheric CO₂. *Science* 284, 1973–1976.