

The growing season carbon balance of a sub-boreal clearcut 5 years after harvesting using two independent approaches to measure ecosystem CO₂ flux

Thomas G. Pypker and Arthur L. Fredeen

Abstract : From 27 June to 3 September 1999, CO₂ fluxes from a 5-year-old, 84.15-ha vegetated clearcut in sub-boreal British Columbia were measured using a Bowen ratio energy balance (BREB) system and a second approach (the component model) that was based on scaled up CO₂-flux measurements from belowground and plants (spruce seedlings and representative deciduous species). Over the 69-day study period both methods estimated the site to be a small sink for CO₂ (−22.4 and −85 g C·m^{−2}, respectively). Differences between the sink size of the two approaches largely resulted from a divergence in the data after 7 August when the BREB data indicated a switch from sink to source approximately 14 days in advance of the same change from sink to source seen in the component model data. The main components of the CO₂ flux within the clearcut were belowground respiration (338 g C·m^{−2}) and deciduous plant photosynthesis (−375 g C·m^{−2}). The conifer seedlings were only a minor component in overall CO₂ flux over the growing season (−48 g C·m^{−2}). The small overall sink estimated for the site for the approximately 2.5-month growing period would likely have been surmounted by the belowground respiration if the yearly CO₂ fluxes had been taken into account. For example, an additional 68 g C·m^{−2} was added to the atmosphere from 3 to 23 September (based on belowground respiration data only), after deciduous plants senesced. This source alone was enough to push the site from a sink to a source for CO₂.

Résumé : Du 27 juin au 3 septembre 1999, les flux de CO₂ dans une coupe à blanc datant de 5 ans, couvrant 84,15 ha et située dans la partie sub-boréale de la Colombie-Britannique ont été mesurés à l'aide d'un système de bilan énergétique basé sur le rapport de Bowen et à l'aide d'une seconde approche (le modèle par composantes) basée sur l'extrapolation de mesures de flux de CO₂ effectuées dans le sol et sous les plantes (semis d'épinette et d'espèces décidues représentatives). Pendant la période de mesure de 69 jours, les deux méthodes ont montré que le site constitue un faible puits de CO₂ (respectivement −22,4 et −85 g C·m^{−2}). La différence dans la taille du puits entre les deux approches est essentiellement le résultat d'une divergence dans les données après le 7 août. Selon les données du bilan énergétique, le puits devenait une source approximativement 14 jours plus tôt que l'indiquaient les données du modèle par composantes. Les composantes principales du flux de CO₂ dans la coupe à blanc provenaient de la respiration souterraine (338 g C·m^{−2}) et de la photosynthèse des plantes décidues (−375 g C·m^{−2}). Pendant la saison de croissance, les semis de conifères représentaient seulement une composante mineure du flux total de CO₂ (−48 g C·m^{−2}). Il est probable que le faible flux négatif aurait été contrebalancé par la respiration souterraine si les flux de CO₂ avaient été pris en compte pour toute l'année. Par exemple, 68 g C·m^{−2} supplémentaires se sont ajoutés à l'atmosphère entre le 3 et le 23 septembre (seulement sur la base de la respiration souterraine), après la sénescence des plantes décidues. Cette seule source est suffisante pour faire basculer le site de l'état de puits à celui de source de CO₂.

[Traduit par la Rédaction]

Introduction

Within the last two centuries, anthropogenic CO₂ emissions have increased the levels of atmospheric CO₂ from 280

to over 360 ppm (Keeling et al. 1996). This rise in atmospheric CO₂ has largely been the result of three sources: burning of fossil fuels, cement manufacture, and land-use change. Landscape modification alone is thought to explain approximately 50% of the rise in atmospheric CO₂ prior to 1980 (Woodwell et al. 1983) and to represent 23% of the rise in the 1980s (Schimel 1995). Most of the rise in CO₂ from land-use change is from timber harvesting (Harmon et al. 1990) and the conversion of forests to agriculture and pasture (Tans et al. 1990).

Attempts to quantify the sources and sinks for CO₂ to the atmosphere have unveiled a large missing carbon sink thought to reside in the Temperate Zone of the Northern Hemisphere (Tans et al. 1990; Ciais et al. 1995). While the size of the missing sink is reasonably well established

Received 4 December 2000. Accepted 11 October 2001.

Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 3 May 2002.

T.G. Pypker¹ and A.L. Fredeen.² Forestry Program, College of Science and Management, University of Northern British Columbia, 3333 University Way, Prince George, BC V2N 4Z9, Canada.

¹Present address: 301A Richardson Hall, Department of Forest Science, Oregon State University, Corvallis, OR 97331, U.S.A.

²Corresponding author (e-mail: fredeena@unbc.ca).

(1.5–2.0 Pg C·year⁻¹), its location has not been resolved (Post et al. 1990; Dale et al. 1991; Sarmiento 1993; Dixon et al. 1994). The inability of researchers to pinpoint the area(s) responsible for the accumulation of carbon displays a lack of information about the carbon in the atmosphere and its interaction with the biosphere.

Several complex large-scale models have been created in an attempt to estimate the fluxes of carbon to and from the atmosphere (Birdsey et al. 1993; Burschel et al. 1993; Heath et al. 1993; Kolochugina and Vinson 1993a; Kolochugina and Vinson 1993b; Melillo et al. 1993; Kurz and Apps 1994; Turner et al. 1995; Cohen et al. 1996). These models are forced to make broad assumptions regarding size and direction of carbon fluxes after disturbance events such as fire, insect outbreak, and timber harvesting (i.e., Burschel et al. 1993; Kolochugina and Vinson 1993b; Kurz et al. 1996). With greater empirical knowledge, perhaps, the magnitude of the assumptions could be reduced.

The obvious impact of timber harvesting on forest carbon budgets is the removal of tree carbon and the loss of tree photosynthesis. With CO₂ uptake reduced, it is generally assumed that forest ecosystems will become a source for carbon to the atmosphere, and only when the trees or associated vegetation have been reestablished will the sites revert back to being a sink (Kurz and Apps 1994). The environment (both climate and microclimate) in which the seedlings are grown is crucial in determining when a clearcut will change from a source to a sink for CO₂. For example, sites that are subjected to waterlogging or drought stress may have inhibited forest regrowth, prolonging the length of time the site acts as a source for CO₂.

The impact soil has on the overall carbon budget is poorly understood because information regarding the world's soil carbon pools are limited. Currently, Post et al. (e.g., 1982) and Zinke et al. (e.g., 1984) are the main sources for information on world soil carbon stores. In the boreal forests, a pool of between 65 and 104 Gt carbon, or eight times the amount of carbon stored in the plant biomass, is stored in the soil. Therefore, the size of the carbon flux from belowground may also determine when a site converts from being a source to a sink for carbon. It is often assumed that soil carbon is reduced in the years following a clearcut because of reduced litterfall from the canopy (Covington 1981; Federer 1984; Kawaguchi and Yoda 1989; Yarie 1993; Olsson et al. 1996; Pennock and van Kessel 1997). However, most studies indicate only a small change in soil carbon stores following tree harvest unless the site is exposed to an intense burn (Johnson 1992).

The main microclimate controls on belowground respiration are moisture and temperature (Kucera and Kirkham 197; Fernandez et al. 1993; Striegl and Wickland 1998). The microorganisms responsible for the decomposition of the organic matter generally demonstrate a positive relationship to moisture and temperature. However, if the temperature of the soil becomes too warm or the moisture increases to a level where the soil is waterlogged, a decrease in respiration may result. Therefore, the microclimate initiated by clearing the forest will heavily influence how soils respond. The removal of trees lowers evapotranspiration and may increase solar radiation at the soil surface (Lewis 1998). These environmental changes may result in an increase in soil moisture

and temperature. However, the increase in soil temperature could also remove more moisture than is gained from the decrease in evapotranspiration, thus leading to drier soils and lower belowground respiration.

In this paper, we attempt to quantify the flux of CO₂ from a 5-year-old sub-boreal clearcut in central British Columbia using two independent methods. The Bowen ratio energy balance (BREB) method is contrasted with another independent estimate, whereby component fluxes are individually measured and modeled using microclimate data and scaled to the ecosystem level using biomass information for the site. There has been very little research on the overall fluxes of CO₂ from very young disturbed forest sites. It is the intent of this paper to not only establish the magnitude of the CO₂ sink or source strength of this 5-year-old sub-boreal clearcut over the growing season but also to determine the relative importance of the component fluxes, from aboveground and belowground components, on the overall carbon budget.

Methodology

The site

We made CO₂ flux measurements in the summer of 1999 from 27 June to 3 September in a clearcut in the University of Northern British Columbia – University of British Columbia Aleza Lake Research Forest (54°01'30"N, 122°07'30"W). An 84.15-ha stand of sub-boreal spruce–fir forest at 710 m a.s.l. was harvested in 1994 and, after mounding, planted with 2-year-old hybrid white spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex Engelm.) with a smaller component of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia*) in 1995. The site is described as SBSwk1-8 (wet, cool subzones of the Sub-Boreal Spruce zone) using the forest ecosystem classification of British Columbia (Meidinger and Pojar 1991). The site is cool and wet and has a relatively high snowfall relative to other areas in the central plateau region of sub-boreal British Columbia (mean annual air temperature 1.7–5.0°C). Snowfall typically accumulates by November and melts by the end of April to early May.

Prior to harvesting the site contained a combination of hybrid white spruce and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) with an understory of *Ribes lacustre* (Pers.) Poir., *Lonicera involucrata* (Richardson) Banks ex Spreng, *Viburnum edule* (Michx.) Raf., *Oplopanax horridus* (J. E. Smith) Miq., and *Rubus idaeus* L. The soils are clay and nutrient rich, sub-hygic and have been classified as Orthic Luvic Gleysols (Arocena and Sanborn 1999). At 5 years post-harvest the site contained 1200 spruce seedlings/ha along with a variety of natural deciduous plants dominated by *Chamerion angustifolium* L., *Spiraea douglasii* ssp. *menziesii* (Hook.) Presl, *Rubus idaeus*, *Ribes lacustre*, *L. involucrata*, *Equisetum arvense* L. Fernald, and a variety of grasses dominated by *Calamagrostis canadensis* Michx.

The site was well suited for the Bowen ratio system approach. The canopy was short (mean height 0.6 m), with few of the seedlings exceeding 1.2 m in height (mean seedling height 0.82 m). The dominant wind direction was from the southwest, and the forest edge was well over 400 m from the

tower in that direction. The tower had a minimum of 300 m of fetch in all directions, well within the recommended 100 m of fetch for every meter in height suggested by others (Horst and Weil 1992; Stannard 1997). In addition, the site was relatively flat with a slope of approximately 1% overall. The 100 × 100 m measurement area was subdivided into a 20 × 20 m grid network and the BREB tripod placed in the center grid square. Gridlines were also used as a trail network to prevent excessive trampling of the site.

Measurement of ecosystem CO₂ flux

Ecosystem CO₂ flux was measured using a commercial Bowen ratio system (023/CO₂, Campbell-Scientific, Edmonton, Alta.) and the Bowen ratio energy balance (BREB) approach (Tanner 1960; Price and Black 1990). The CO₂ gradient was measured from 27 June to 3 September 1999 by means of a closed-path CO₂-H₂O analyzer (LI-6262, LICOR Inc., Lincoln, Nebr.) connected to intake tubes situated in arms off the instrument tripod. The top arm of the Bowen ratio system was 2.5 m above ground level and the bottom arm was situated 1.4 m directly beneath it. Flow rates through the system tubing were maintained at 700–800 cm³·min⁻¹. Every 2 min the air drawn in through the intake tubes was reversed between the reference and sample cells of the infrared gas analyzer (IRGA), and 40 s was allowed for the pump to purge the IRGA and resume measurements. The mean CO₂ gradients were calculated every 20 min. At the beginning of every hour, one cell of the IRGA was scrubbed to establish the absolute concentrations of CO₂ and H₂O, because during the rest of the hour, air from either the upper or lower arm was flowing through the reference cell of the IRGA. The hourly scrub related the millivolt signal to the concentration of CO₂ in each cell within the IRGA. The system was calibrated, at a minimum, two times per week.

The energy balance for the site was determined based on BREB system measures of net radiation (Q^*) and its components sensible heat (H), latent heat (LE), and ground heat flux (G). The Q^* was measured every 10 s with a Q7 net radiometer (Campbell Scientific) that was mounted over a representative surface (2.8 m in height) and averaged over a 20-min interval. To establish the temperature gradient 75- μ m chromel-constantan fine-wire thermocouples were placed at the end of each arm. The ground heat flux was estimated using two heat flux plates (HFT-3, Campbell Scientific) each inserted 6 cm below the surface of the ground in conjunction with thermocouple probes (TCAV, Campbell Scientific) placed 4 cm above and 2 cm below each plate. The four leads of the thermocouple averaged the temperature changes between 2 and 8 cm of depth within the soil column.

Calculation of energy and CO₂ fluxes

All BREB calculations were performed using the computer program SPLIT (PC208 Software, Campbell Scientific). In brief, G was calculated in three steps. First, soil characteristics were used to calculate c_s , the heat capacity (J·m⁻³·K⁻¹) of the moist soil:

$$[1] \quad c_s = \rho_b(c_d + \theta_m c_w)$$

where ρ_b (kg·m⁻³) is the bulk density of the soil, c_d (J·kg⁻¹·K⁻¹) is the specific heat of a dry mineral soil, θ_m (no units) is percent water content on a mass basis, and c_w (J·kg⁻¹·K⁻¹) is the specific heat of water. Second, the rate of energy storage between the thermocouples belowground (S) (W·m⁻²) over each 20-min interval was then calculated:

$$[2] \quad S = \frac{\Delta T_s c_s d}{t}$$

where ΔT_s (K) is the change in soil temperature, d (m) is the depth of the sensors, and t is time. The G values were then calculated by summing S and the heat flux (W·m⁻²) values provided by the heat flux plates (G_g) (W·m⁻²):

$$[3] \quad G = G_g + S$$

Flux densities of LE, H , and CO₂ (F_C) through the atmosphere above the clearcut were calculated based on the following equations that have been used by others (e.g., Price and Black 1990):

$$[4] \quad LE = \frac{-L_v K_E \partial \rho_v}{\partial z}$$

$$[5] \quad H = \frac{-\rho C_p K_H \partial T}{\partial z}$$

$$[6] \quad F_C = \frac{-K_C \partial \rho_C}{\partial z}$$

where K_E , K_H , and K_C are the eddy diffusivities for water vapour, heat, and CO₂ respectively; ρ_v (kg·m⁻³) is water vapour density; ρ_C (kg·m⁻³) is CO₂ density; ρ (kg·m⁻³) is air density; C_p (J·kg⁻¹·K⁻¹) is the heat capacity of air; L_v (J·kg⁻¹) is the latent heat of vapourization; T (K) is the absolute air temperature; and z (m) is height.

Using the universal gas law, eqs. 4 and 6 can be transformed to

$$[7] \quad LE = -L_v K_E \frac{PM_w \partial W}{TR \partial z}$$

$$[8] \quad F_C = -K_C \frac{PM_C \partial C}{TR \partial z}$$

where P (kPa) is pressure, M_w (g·mol⁻¹) is the molecular weight of water, W is the mole fraction of water to air, R (J·kg⁻¹·mol⁻¹) is the universal gas constant, M_C (g·mol⁻¹) is the molecular weight of CO₂, and C is the mole fraction of CO₂ to air.

The BREB system estimates the fluxes of H , LE, and F_C through a number of steps beginning with the simplified energy balance equation:

$$[9] \quad Q^* = H + LE + G$$

the similarity assumption ($K_H = K_E = K_C$) (Monteith and Unsworth 1990) and the Bowen ratio. The Bowen ratio, defined as the ratio of sensible to latent energy, was calculated by

$$[10] \quad \beta = \frac{H}{LE} = \frac{C_p \partial T}{L_v \epsilon \partial W}$$

where ∂T (K) is the temperature gradient and ϵ is the ratio of molecular weight of water vapour to dry air. Combining eqs. 9 and 10 to eliminate LE gives the following equation for H :

$$[11] \quad H = \frac{\beta(Q^* - G)}{1 + \beta}$$

Using H from eq. 11, the eddy diffusivity for CO_2 was estimated by rewriting eq. 5 in finite form as follows:

$$[12] \quad K_C = K_H = \frac{(z_1 - z_2)H}{(T_1 - T_2)\rho C_P}$$

Then, eq. 8 was used in finite form to calculate the CO_2 flux. The fluxes of CO_2 were corrected using the equations established by Webb et al. (1980). In keeping with biometeorological convention, positive fluxes of F_C , LE, and H are used to indicate movement away from the surface and negative toward the surface.

Other meteorological measurements

Additional meteorological variables were measured at the site. Wind speed and direction were estimated using a wind sensor placed at the top of the tower (3.0 m) (R.M. Young Wind Sentry, Campbell Scientific). Light levels were taken at 1.9 m using a quantum sensor (LI-COR quantum sensor, LI-COR Inc., Lincoln, Nebr.). Four thermocouples (chromel-constantan), two at 10 cm and two at 15 cm depth, were inserted into the soil to increase the spatial sampling of soil temperature for modeling purposes. The soil and light measurements were taken every minute and then averaged over 20 min. Lastly, air temperature and relative humidity were measured at 1.7 m with a single probe (HMP35C, Campbell Scientific) every 10 s and then averaged over 20 min. All the data were stored on two data loggers (21X, Campbell Scientific) and downloaded to a field-portable laptop computer as required.

Conifer photosynthesis

At the beginning of the field season, the mean heights of the spruce seedlings were calculated and 20 randomly selected seedlings that were within 1 SD of the mean were selected. A 1-year-old branchlet and either a 3-year-old, 2-year-old, or a second 1-year-old branchlet were selected for photosynthesis measurements on either the north or south side of the seedlings.

Photosynthesis and respiration measurements were made using a portable closed gas-exchange system (LI-6200, LI-COR Inc.) on a weekly basis between 08:00 and 20:00. Microclimate variables of light (photosynthetically active radiation, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (LI-COR quantum sensor, LI-COR Inc.), relative humidity, air temperature, and atmospheric water vapour content were measured by the LI-6200 while soil temperature (Reotemp instruments, San Diego, Calif.) and soil moisture (kg H_2O /kg soil) (Nie-Co-Product Nieuwkoop B.V., Aalsmeer, Holland) were made independently but simultaneous with gas-exchange measurements. Microclimate variables were later used in regression models to establish relationships that were used to estimate carbon uptake (see below).

Deciduous plant photosynthesis

The deciduous plants on site leafed out around 31 May. Throughout the field season photosynthetic and respiration rates of *Chamerion angustifolium*, *S. douglasii* spp. *menziesii*, *L. involucreta*, and *Calamagrostis canadensis*, were measured with the LI-6200 (as above) under varying microclimate conditions between 08:00 and 20:00. The plants were randomly selected on each measuring day within the study area. Area-based photosynthesis was based on one side of the leaf area as determined by leaf traces on transparent acetate sheets.

Soil CO_2 flux measurements

Six pairs of polyvinylchloride collars (9.55 cm in diameter) were placed in randomly selected grid squares throughout the measurement area. Measurements were taken using the LI-6200 with the soil chamber attachment (model No. 6000-09, LI-COR Inc.) as in Norman et al. (1992) on a weekly basis between 08:00 and 20:00. During the soil measurements both soil temperature (model No. 6000-09TC, LI-COR Inc.) and moisture (as above) were taken at a depth of 10 cm.

Biomass

On 7–8 July and 17–18 August, the aboveground living biomass for the deciduous plants was destructively sampled in 24 randomly selected 1-m² plots within the measurement grid. On 25 September, the aboveground components of 20 *P. glauca* × *P. engelmannii* seedlings were randomly selected and removed from the site. The seedling branchlets were further divided up into their individual ages and, along with conifer stem and deciduous samples, dried at 65°C for 72 h and weighed.

System flux estimates based on component fluxes

Extrapolations from instantaneous component fluxes to the ecosystem scale were made using regression relationships between component gas-exchange and microclimate data. The ecosystem flux was composed of four primary components: conifer, herbaceous deciduous plant, woody deciduous plant (shrub), and belowground respiration. Multiple regressions relating CO_2 flux from the four components to microclimate variables were established using the best subset method and the R^2 difference test ($p = 0.05$). The regressions provided estimates of the CO_2 fluxes in micromoles C per square metre leaf or ground area per second.

The component model required four steps to scale from the leaf to the clearcut. First, the leaf area to leaf biomass ratios (specific leaf area) were calculated for representative conifer needles and herbaceous and woody plant leaves. Second, specific needle and leaf areas were multiplied by the needle or leaf biomass totals per unit ground area in the clearcut ($\text{g}\cdot\text{m}^{-2}$) taken throughout the study period to estimate the leaf area per square metre for each plant component. Third, component-level CO_2 fluxes were extrapolated temporally by using continuous micrometeorological information from the Bowen ratio tower in conjunction with the multiple regression equations (Table 1). Finally, estimates from the multiple regressions were multiplied by the leaf area calculated in the second step, producing the carbon flux estimates for the different plant components on a per square

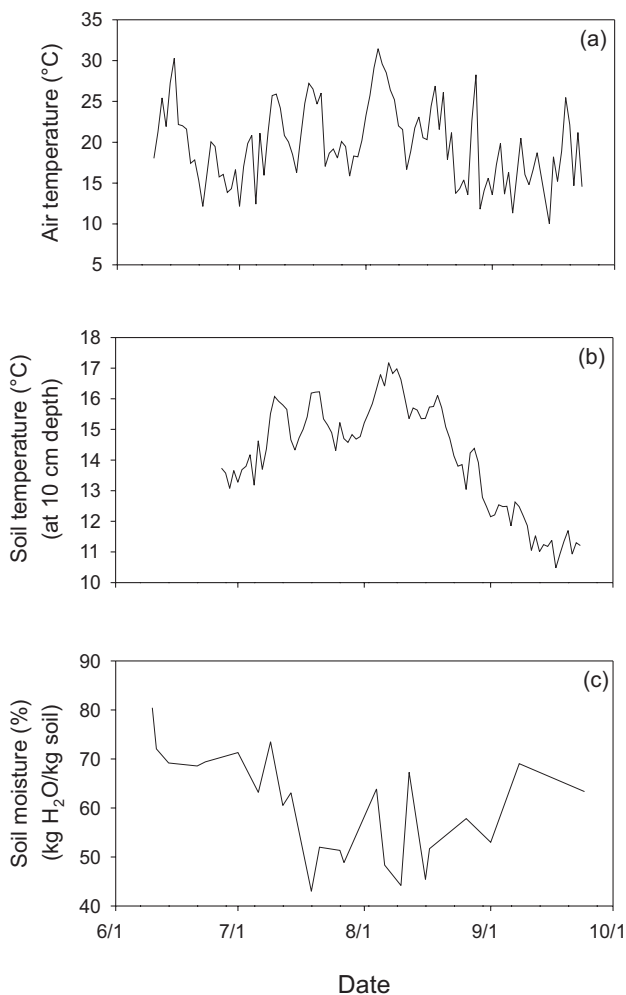
Table 1. Multiple regression equations for estimation of component CO₂ fluxes (belowground respiration (*R*) and net photosynthesis (*P_n*) by plant type, day of year and time of day) in a 5-year-old clearcut in the Aleza Lake Research Forest, British Columbia.

Component flux	<i>n</i>	Regression equation (μmol C·m ⁻² ·s ⁻¹)*	<i>R</i> ²	SE
Belowground	115	$R = 0.953 + 0.354A - 0.0198D$	0.66	0.978
Conifer (day)	447	$P_n = -1.61 - 0.22A - 1.8 \ln(B) + 0.323C$	0.76	2.74
Conifer (night)	77	$R = 0.056C / (1 - 0.01918C)$	0.72	0.915
Herbaceous plants (day)	99	$P_n = -7.89 - 0.666A - 1.88 \ln(B) - 0.0247C + 0.0416E + 0.007291F$	0.53	3.30
Herbaceous plants (night)	29	$R = -0.534 - 0.137A + 0.161C + 0.0202G$	0.81	0.465
Woody plants	47	P_n and $R = -4.72 - 1.26 \ln(B) + 0.239C$	0.77	1.77

Note: Multiple regressions were established using the best subset method and are based upon a square metre ground area when estimating soil CO₂ efflux and square metre leaf area when estimating leaf CO₂ flux. *A*, soil temperature; *B*, quantum flux; *C*, air temperature; *D*, soil moisture; *E*, day of year; *F*, time of day; *G*, relative humidity.

*All regression equation variables were significant at the 0.95 level.

Fig. 1. Maximum daily (a) air temperature, (b) soil temperature, and (c) mean soil moisture from 14 June to 23 September 1999 for a clearcut in the Aleza Lake Research Forest, British Columbia (54°01'30"N, 122°07'30"W).



metre basis. When modeling the plant photosynthetic and respiration rates it was assumed that 15% of leaf photosynthesis was lost to stem respiration (Ryan et al. 1994; Levy and Jarvis 1998). The belowground CO₂ flux estimates were already in square metres. Hence, the belowground CO₂ fluxes were estimated based on the regressions and the

micrometeorological values given by the tower. Upon completing the CO₂ flux estimates for each component, the overall flux of the site was estimated for 20-min intervals using

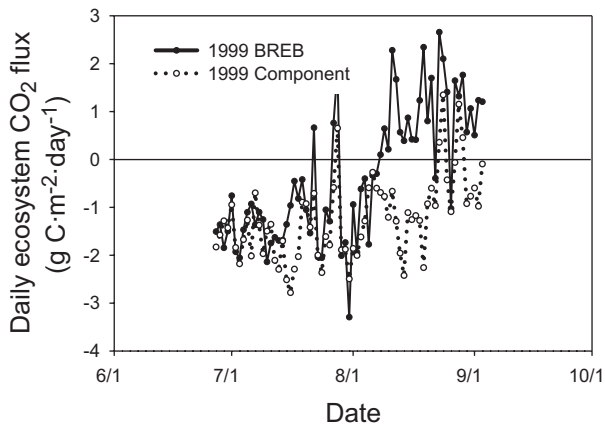
$$[13] \quad F_C = F_{\text{conifers}} + F_{\text{herbaceous plants}} + F_{\text{woody plants}} + F_{\text{belowground}}$$

Corrections of BREB data

To estimate a continuous CO₂ flux for the cut block, various corrections of the BREB data were necessary. The site itself, with its shallow slope and large area of fairly uniform terrain and vegetation, was suitable for the BREB approach. However, the data did suffer from the typical problem of poor estimates for dusk, dawn, and most nighttime periods, as well as rainy days (Tanner 1960). The problem periods around dusk and dawn were common but occurred over a short time period, often for less than an hour. Hence, these values were systematically replaced by extrapolating from BREB CO₂ fluxes immediately surrounding the problem periods (Baldocchi et al. 1997; Ham and Knapp 1998). In contrast, during longer periods of equipment failure or extended rain events, CO₂ fluxes were estimated using a regression with light from the days immediately surrounding the missing data. The regression was then used to fill in the gaps in the data (Ham and Knapp 1998). Of the total measurement days, 30% required the use of regressions to fill in lost data.

Nighttime CO₂ fluxes were overestimated because of stratification of the atmosphere as evidenced from high CO₂ concentrations and low wind speeds at the tripod level. Stratification is problematic, because the assumption of equivalence of eddy diffusivity coefficients may not hold true (Verma et al. 1978; Angus and Watts 1984). In addition, the small *Q** values associated with nighttime flux estimations can further exacerbate the problem by inaccurately estimating the eddy diffusivity coefficient resulting in an exaggeration of the CO₂ flux (Price and Black 1990). The nighttime values for the BREB method were extremely poor because of low wind speeds. Therefore, a strict criteria was used to edit data. In conditions when stratification was a problem (lower arm 2 μmol·mol⁻¹ greater than the upper arm) and (or) the net radiation values were low (between -20 and 20 W·m⁻²), the component flux approach estimates of ecosystem flux were used in place of BREB nighttime estimates. This resulted in the replacement of almost all nighttime BREB data.

Fig. 2. Comparison of Bowen ratio (BREB) and component model daily flux estimates (Table 1) for a 5-year-old clearcut from 27 June to 3 September 1999 in the Aleza Lake Research Forest, British Columbia. Values are similar from 27 June to 7 August after which the two estimates diverge for approximately 14 days. BREB data was corrected with component model data for nighttime periods.



Results

Physical environment

The summer of 1999 was cool with few periods of warm weather (Fig. 1a). During the study period, the daily high air temperatures ranged from a low of 12.2°C on 1 July to a high of 31.4°C on 6 August. The mean daily temperature over the study period was 13.3°C. Soil temperatures remained between 13 and 15°C for the month of July and peaked at 17.2°C on 7 August. Between 5 May and 24 September the soil remained moist, with levels ranging between 43% on 4 July to a high of 72% on 10 June. Hence, the site was cool during the study period and the soil remained moist for most of the summer.

Microclimate variables and the ecosystem component CO₂ flux

The component fluxes correlated well with microclimate variables. Conifer net photosynthesis correlated well with the microclimate variables of light, soil temperature, and air temperature producing an R^2 of 0.76 (Table 1). Conifer night respiration was well described by air temperature alone ($R^2 = 0.72$). Estimation of CO₂ exchange in herbaceous plants, based on gas-exchange measurements on *Chamerion angustifolium*, required two separate regressions. Light, soil moisture, and soil temperature were used to estimate photosynthesis, while air temperature, relative humidity, and soil temperature were used to estimate nighttime CO₂ fluxes. Woody deciduous plant carbon uptake was adequately described by a single equation based on the variables light and air temperature for the entire study period. The woody plant regression was established using measurements on *S. douglasii* spp. *menziesii*. Belowground respiration was well correlated with soil moisture and soil temperature at 10 cm depth.

Table 2. Herbaceous and woody biomass for deciduous vegetation early (7–8 July 1999) and late (17–18 August 1999) in the growing season in a 5-year-old clearcut in the Aleza Lake Research Forest, British Columbia.

Date	Herbaceous plant (g·m ⁻²)	Woody plant (g·m ⁻²)	Total (g·m ⁻²)
7–8 July	95	48	143
17–18 August	125	64	189
Biomass increase	30	16	46

Note: The woody estimates are leaf biomass only.

Table 3. Carbon allocation in the stems and needles of interior spruce seedlings from a 5-year-old clearcut in the Aleza Lake Research Forest, British Columbia.

Needle age-class (years)	Stems (g·m ⁻²)	Needles (g·m ⁻²)	Total (g·m ⁻²)
<1	4.34	10.6	14.9
>1	19.9	10.6	30.5
Total	24.2	21.2	45.4

Note: The biomass was sorted according to the age-class of the needles.

Change from sink for CO₂ to source for CO₂ in early August

The clearcut rapidly changed from a sink to a source in early August (Fig. 2). The days prior to the crossover point were quite warm (Fig. 1), and the plants were beginning to set seed and senesce. Prior to the downturn in photosynthetic uptake of CO₂ the BREB approach estimated CO₂ fluxes that were only 0.005 mg C·m⁻²·s⁻¹ greater (more positive) than the component model, but the difference increased to 0.033 mg C·m⁻²·s⁻¹ after 7 August. The difference in fluxes before and after 7 August was significant at the 99% confidence level ($p < 0.001$).

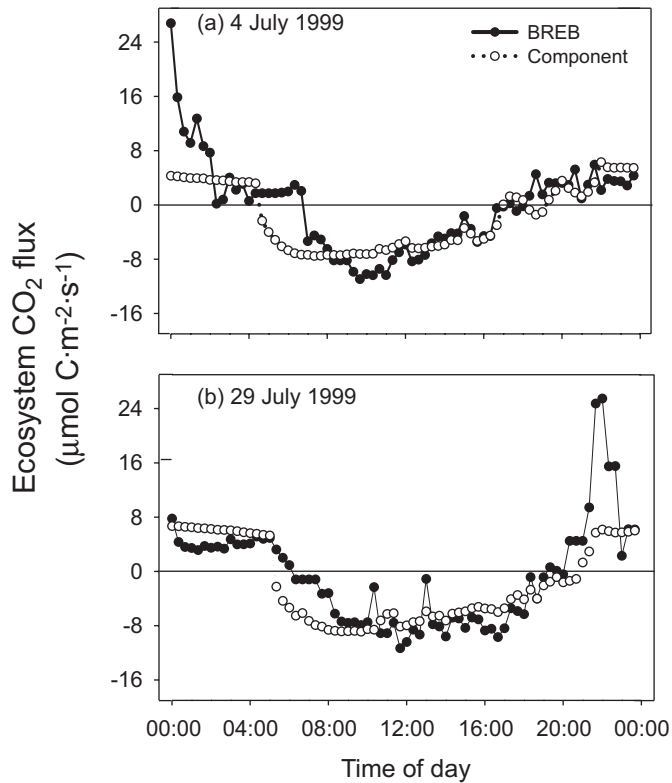
Biomass

The deciduous plants were a much more important sink for CO₂ over the summer than the coniferous plants. The deciduous plants began to leaf out on approximately 1 June and by the middle of August the plants had accumulated over 189 g·m⁻² of new aboveground biomass (the whole aboveground parts of the herbaceous plants and leaves only for woody plants) (Table 2). By this date most of the deciduous plants had set seed and begun to senesce. The conifers had a planting density of 1200 stems/ha and averaged 379 g/seedling. By the end of the growing season the conifers had only allocated 14.9 g·m⁻² of new growth to stems and needles (Table 3). In total, plants produced 204 g·m⁻² of aboveground biomass, with >90% of the new aboveground biomass resulting from deciduous plants.

The BREB method and component model estimates of ecosystem CO₂ fluxes

The component model agreed with the BREB method during the day, but their estimates diverged at night. Typical flux estimates for the clearcut from the component model and BREB methods are shown for 4 July and 29 July 1999 (Figs. 3a and 3b). For sake of contrast, and to illustrate the

Fig. 3. The estimated CO₂ fluxes using the BREB and component model approaches for (a) 4 July and (b) 29 July 1999 in a 5-year-old clearcut within the Aleza Lake Research Forest, British Columbia. For the sake of contrast, the BREB nighttime estimates have not been corrected.



problems with nighttime measurement, the BREB nighttime fluxes were not corrected using component model data in these figures. However, by substituting the component model nighttime estimates for poor predictions by the BREB method, the estimated CO₂ efflux from the site is much diminished resulting in both approaches estimating similar daily CO₂ losses or gains for the study area prior to 7 August (Fig. 2). Subsequent to 7 August, the BREB estimates switched from a sink to a source for CO₂, but the component model lagged behind indicating a site transition from sink to source a full 14 days later.

After making nighttime corrections to the BREB data, both the component model and BREB approaches estimated the clearcut to be a sink over the 69-day measurement period (-85 and -22.4 g C·m⁻², respectively) (Table 4). Component fluxes indicated that herbaceous and woody plants absorbed the bulk of the carbon removing 210 and 165 g C·m⁻², respectively. In comparison, the conifers only removed an estimated 45 g C·m⁻² or eight times less than the deciduous plants. Belowground respiration acted as a constant CO₂ source throughout the season. From 27 June to 3 September the roots and soil flora and fauna released 338 g C·m⁻², thereby counteracting most of the carbon sink generated via plant photosynthesis.

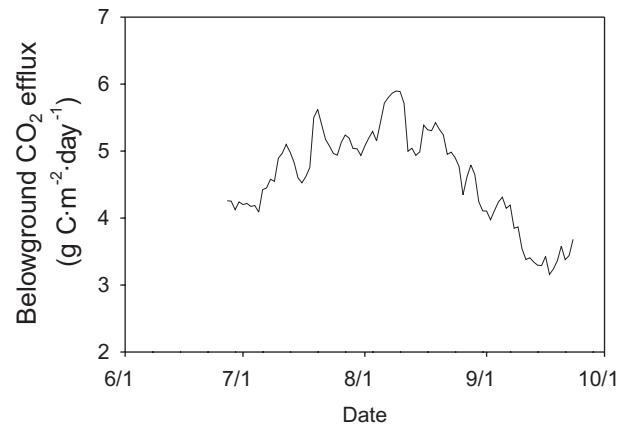
Belowground CO₂ efflux

Belowground CO₂ efflux was sizable both during the growing season (4.12 – 5.89 g C·m⁻²·day⁻¹) (Table 4) and for

Table 4. Seasonal estimates of CO₂ accumulation in the various components using the component model from 27 June to 3 September 1999 in a 5-year-old clearcut at the Aleza Lake Research Forest, British Columbia.

Component	Component model (g C·m ⁻²)	BREB method (g C·m ⁻²)
Conifers	-48	—
Herbaceous plants	-210	—
Woody plants	-165	—
Belowground	338	—
Total	-85	-22.4

Fig. 4. Belowground efflux of CO₂ from 27 June to 23 September 1999 from a 5-year-old clearcut in the Aleza Lake Research Forest, British Columbia. Belowground efflux totaled 68 g CO₂·m⁻² during the 19 days following the last Bowen ratio ecosystem flux measurement.



measurement dates following the study period (3.16 – 4.2 g C·m⁻²·day⁻¹) (Fig. 4). In fact, belowground respiration from 4 through 23 September, a time when herbaceous plants were without foliage and woody plants mostly senescent, contributed a further 68 g C·m⁻² to the atmosphere (Fig. 4), enough to convert the site into an overall source for CO₂.

Discussion

BREB flux estimates

The component model and BREB methods produce very similar flux estimates during daylight hours. Daytime estimates were very comparable (Figs. 3a and 3b) as were the corrected daily fluxes until approximately 7 August (Fig. 2). The two models diverged after 7 August with the BREB method estimating the site to be a larger source for CO₂ than the component model. The major problem associated with the component model was its reliance on measured leaf-level CO₂ fluxes that were only measured once or twice every 2 weeks. A rapid decrease in photosynthetic uptake due to senescence, flowering and seed set, heat stress or frost damage could not be accommodated by the discrete sampling regime associated with the component model approach. As a result, the component model estimated the clearcut to be a larger sink for CO₂ than the BREB method.

Both approaches estimated the site to be a sink for CO₂ for the 69-day study period (Table 4). The component model's estimate is likely too large because of its inability to interpolate fluxes during the 2 weeks subsequent to 7 August. Prior to 7 August, the discrepancy between the BREB method and the component model was only 0.005 mg C·m⁻²·s⁻¹, but after 7 August the difference increased to 0.033 mg C·m⁻²·s⁻¹. While this difference appears small difference, it was significant enough to result in a sink of -22 g C·m⁻² for the BREB method versus -85 g C·m⁻² for the component model.

The carbon uptake estimated by the component model for deciduous plants was in line with aboveground biomass carbon measured. If we assume that biomass is 50% carbon, aboveground biomass of 204 g·m⁻² would translate into 102 g C·m⁻². In comparison, the component model estimates that between 27 June and 18 August, the plants absorbed 342 g C·m⁻². Assuming 50% of CO₂ uptake went into belowground biomass (Raich and Nadelhoffer 1989; Broderick 1990) and 55% of the remainder was lost to respiration (Waring et al. 1998), the component model would estimate an uptake of 77 g C·m⁻². These values are relatively close considering the assumptions involved and the loss of biomass through seeds, flowers, stem growth, and leaf turnover was not captured, and a portion of the growing season between 1 and 26 June was missed.

Following 3 September the deciduous plants senesced and the conifers hardened off for the winter, but CO₂ efflux from belowground continued (Fig. 4). Belowground respiration emitted an estimated 68 g C·m⁻² between 3 September and 23 September alone, and the efflux of CO₂ would have continued, albeit at a reduced rate, under the snowpack (Coxson and Parkinson 1987; Sommerfeld et al. 1993; Clein and Schimel 1995; Evans et al. 1998). The snow insulates the soil, buffering it against the colder air temperatures thereby allowing for greater belowground respiration (Bleak 1970; Moore 1983). A study conducted during the winters of 1997 and 1998 by Evans et al. (1998) within the Aleza Lake Research Forest at a site with an identical site class (SBS week1-8) observed winter fluxes from between 0.60 to 0.77 g C·m⁻²·day⁻¹. Others have measured similar winter CO₂ fluxes of between 0.41 to 0.77 g C·m⁻²·day⁻¹ (Sommerfeld et al. 1993) and 0.20 to 0.82 g C·m⁻²·day⁻¹ (Coxson and Parkinson 1987) in southeastern Wyoming and southwestern Alberta, respectively.

Using the values from Evans et al. (1998) the loss of CO₂ from the site can roughly be estimated to be between 83 and 121 g C·m⁻²·year⁻¹. The estimate contains four specific assumptions: CO₂ losses range between 0.60 and 0.77 g C·day⁻¹ under the snowpack (1 November to 30 April); fluxes linearly decreased to the winter flux in the fall (4 September to 31 October); fluxes decreased from the winter flux to a net uptake of -1.41 g C·day⁻¹ in the spring (1 May to 1 June) when the site flushed (-1.41 g C·day⁻¹ is the average daily C flux from 27 June to 5 July); and after June 1 the flux remained at -1.41 g C·day⁻¹ until 27 June when the BREB flux estimates resumed. While the assumptions do not provide a confident estimate of the annual ecosystem C flux, it does demonstrate that the loss of CO₂ from belowground during the winter months (109-139 g C·m⁻²) is enough to surmount any gain by the plants during the summer months.

Considering the size of the CO₂ efflux from belowground in the years immediately following timber harvest, the relatively larger CO₂ uptake by the deciduous plants to coniferous plants becomes important. If the loss of CO₂ in the years immediately following timber harvest is to be reduced, an attempt must be made to minimize the removal of deciduous plants by mechanical and chemical brushing. Clearly, a balance must be established between reestablishing the conifers and supporting the deciduous plants present.

The component CO₂ fluxes

Mid-day conifer photosynthesis was similar to rates measured by others under a variety of conditions (Watts and Neilson 1978; Bassman 1989; Man and Lieffers 1997), typically ranging between 5 and 9 μmol C·m⁻²·s⁻¹ depending on the climate and microclimate. The deciduous plants had much higher mid-day photosynthetic rates than in conifers, typically ranging from between 6 and 16 μmol C·m⁻²·s⁻¹ depending on the species and the micrometeorological conditions.

Belowground CO₂ efflux, between 27 June and 23 September, totaled 406 g C·m⁻², with values ranging from 3.16 to 5.90 g C·m⁻²·day⁻¹. Other studies involving recently cleared forest have found fluxes that were comparable with our values (Edwards 1975; Ewel et al. 1987; Gordon et al. 1987). However, some studies have estimated CO₂ fluxes that were lower than those found in this study (Weber 1990; Fernandez et al. 1993; Lytle and Cronan 1998; Striegl and Wickland 1998). This variation is likely due to site-specific constraints on soil respiration and (or) plant productivity. The high moisture levels (rarely below 50%) and relatively high nutrient status of the site may have enhanced decomposition and root activity (Fig. 1).

The overall CO₂ fluxes in comparison to other northern forests

The observed BREB method fluxes of -0.05 to -0.21 mg C·m⁻²·s⁻¹ (based on 20-min averages for July and early August) between 09:00 and 15:00 in this study are similar to those found in the literature for young clearcuts and some mature stands. For example, Price and Black (1990) found daytime (09:00 and 15:00) CO₂ fluxes above a juvenile Douglas-fir stand during 24 and 29 July and 4 August to be -0.05 to -0.14 mg C·m⁻²·s⁻¹ (from 30-min averages). The main difference between the Douglas-fir stand and the planted spruce clearcut was that the former was a source for CO₂ for a longer period of the day. This may have resulted from drier conditions and shorter summertime daylight hours at the lower latitude site used in the Price and Black (1990) study. Similarly, during the month of July 1996, Valentini et al. (2000) measured the CO₂ exchange above a 12-year-old regenerating boreal forest in central Siberia and found it to be a small sink for CO₂ (-0.093 g C·day⁻¹) during two measurement periods (6-15 and 21-26 July).

The maximum CO₂ uptake rate observed for the clearcut was ≈0.22 mg C·m⁻²·s⁻¹, but it averaged approximately 0.11 mg C·m⁻²·s⁻¹ at mid-day across the study period. Mature stands in the boreal forest tend to have equivalent or lower fluxes of CO₂ when compared with the clearcut in this study. Values of growing season fluxes in high-latitude forests

range from maximum values of $0.15 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in an ecotonal boreal forest to a minimum of $0.049 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in a Siberian larch forest (Hollinger et al. 1998, 1999). Maximum CO_2 uptake for Canadian boreal forests average between $\approx 0.084 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Jarvis et al. 1997) at the southern BOREAS black spruce site to $\approx 0.095 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in a black spruce – lichen woodland near Schefferville, Que. (Fan et al. 1995), and a jack pine forest in central Saskatchewan (Baldocchi et al. 1997). A deciduous aspen site within the boreal forest attained net CO_2 uptake rates of $\approx 0.24 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Black et al. 1996), and this is closer to the maximum values found in this study. Deciduous plants performed the majority of the CO_2 uptake in the clearcut, and they tended to have a greater ability to absorb CO_2 over the short term than the conifer seedlings. However, the growing season for deciduous plants is shorter, because they are not able to take advantage of climatically favourable days in spring and autumn. The site's transition from being a sink to a source was rapid in early August, possibly as a result of increased deciduous plant respiration from seed production and (or) respiration and senescence associated with high air temperature at that time. Given the low growing season sink strength calculated for the clearcut, year-to-year variations in climate could dictate whether such sites act as a source or sink for CO_2 .

While there is little information that is useful regarding boreal or sub-boreal cut block carbon budgets, there is a growing body of information on mature forests. Recently, it has been found that northern mature forests may be tenuously balanced between being a carbon source or sink. For example, Goulden et al. (1998), demonstrated that a boreal black spruce site was a source for CO_2 over the span of 1 year ($\approx 70 \text{ g C}\cdot\text{m}^{-2}$ for October 1994 to October 1995 and $\approx 20 \text{ g C}\cdot\text{m}^{-2}$ for October 1995 to October 1996) but a sink over the year from October 1996 to October 1997 ($\approx 10 \text{ g C}\cdot\text{m}^{-2}$). Furthermore, Lindroth et al. (1998), found that a forest in Sweden lost $\approx 90 \text{ g C}\cdot\text{m}^{-2}$ between 1 June 1994 and 31 May 1995 and $\approx 60 \text{ g C}\cdot\text{m}^{-2}$ during the same period in 1995–1996.

Conclusion

Over the study period, roughly coinciding with the growing season, the vegetated clearcut in this study acted as a small sink for CO_2 . However, if estimates for belowground fluxes for the entire year are considered, losses of CO_2 from the soil would easily exceed that taken up through photosynthesis by deciduous “brush” species and conifers at the site. The conifer seedlings, because of their small biomass, were only a small contributor to the overall carbon budget for the clearcut. It was the deciduous plants that acted as the primary sink for CO_2 for the clearcut, even after 4 years of conifer growth. For this reason, mechanical (brushing) or herbicidal removal of deciduous (“noncrop”) vegetation after clear-cutting should be avoided if our goal is to minimize the accumulation of greenhouse gases in atmosphere during the years immediately after forest harvest.

Acknowledgements

The authors thank Shawn Dagenais and Sandra Wawryszyn for their assistance in field sampling and labora-

tory analysis and Dr. Chris Hawkins and Dr. Peter Jackson for their help in research design. We extend special thanks to Dave Coopersmith for providing our project with the Bowen ratio and LI-6200 systems. Funding for this study was provided by Natural Sciences and Engineering Research Council. We also thank Mike Jull, Dr. Paul Sanborn, and Canadian Forest Products Ltd. for their assistance in finding a suitable research site.

References

- Angus, D.E., and Watts, P.J. 1984. Evapotranspiration—how good is the Bowen ratio method? *Agric. Water Manage.* **8**: 133–150.
- Arocena, J.M., and Sanborn, P. 1999. Mineralogy and genesis of selected soils and their implications for forest management in central and northeastern British Columbia. *Can. J. Soil Sci.* **79**: 571–592.
- Baldocchi, D.D., Vogel, C.A., and Hall, B. 1997. Seasonal variation of carbon dioxide exchange rates above and below a boreal jack-pine forest. *Agric. For. Meteorol.* **83**: 147–170.
- Bassman, J.H. 1989. Influence of two site preparation treatments on ecophysiology of planted *Picea engelmannii* × *glauca* seedlings. *Can. J. For. Res.* **19**: 1359–1370.
- Birdsey, R.A., Plantinga, A.J., and Heath, L.S. 1993. Past and prospective carbon storage in United States forests. *For. Ecol. Manage.* **58**: 33–40.
- Black, T.A., den Hartog, G., Neumann, H.H., Blanken, P.D., Yang, P.C., Russell, C., Nestic, Z., Lee, X., Chen, S.G., Staebler, R., and Novak, M.D. 1996. Annual cycles of water vapour and carbon dioxide fluxes in and above a boreal aspen forest. *Global Change Biol.* **2**: 219–229.
- Bleak, A.T. 1970. Disappearance of plant material under a winter snow cover. *Ecology*, **51**: 915–917.
- Broderick, D.H. 1990. The biology of Canadian weeds. 93. *Epilobium angustifolium* L. (Onagraceae). *Can. J. Plant Sci.* **70**: 247–259.
- Burschel, P., Kürsten, E., Larson, B.C., and Weber, M. 1993. Present role of the German forests and forestry in the national carbon budget and options to its increase. *Water Air Soil Pollut.* **70**: 325–340.
- Ciais, P., Tans, P.P., Trolier, M., White, J.W.C., and Francey, R.J. 1995. A large north hemisphere terrestrial CO_2 sink indicated by the $^{13}\text{C}/^{12}\text{C}$ ratio of atmospheric CO_2 . *Science (Washington, D.C.)*, **269**: 1098–1102.
- Clein, J.S., and Schimel, J.P. 1995. Microbial activity of tundra and taiga soils at sub-zero temperatures. *Soil Biol. Biochem.* **27**: 1231–1234.
- Cohen, W.B., Harmon, M.E., Wallin, D., and Fiorella, M. 1996. Two decades of carbon flux from forests of the Pacific Northwest estimates from a new modeling strategy. *Bioscience*, **46**: 836–844.
- Covington, W.W. 1981. Changes in forest floor organic matter and nutrient content following clear cutting in northern hardwoods. *Ecology*, **62**: 41–48.
- Coxson, D.S., and Parkinson, D. 1987. Winter respiratory activity in aspen woodland forest floor litter and soils. *Soil Biol. Biochem.* **19**: 49–59.
- Dale, V.H., Houghton, R.A., and Hall, C.A.S. 1991. Estimating the effects of land-use change on global atmospheric CO_2 concentrations. *Can. J. For. Res.* **21**: 87–90.
- Dixon, R.K., Brown, S., Houghton, R.A., Solomon, A.M., Trexler, M.C., and Wisniewski, J. 1994. Carbon pools and flux of global forest ecosystems. *Science (Washington, D.C.)*, **263**: 185–190.

- Edwards, N.T. 1975. Effects of temperature and moisture on carbon dioxide evolution in a mixed deciduous forest floor. *Soil Sci. Soc. Am. Proc.* **39**: 361–365.
- Evans, R.E., Lousier, J.D., Massicotte, H.B., and Coxson, D.S. 1998. Winter carbon dioxide evolution and soil temperatures in sub-boreal spruce forests in central British Columbia. *In* Conference Proceedings, Ecology and Management of Northern Forest Soils. University of Northern British Columbia, Prince George, B.C. pp. 203–222.
- Ewel, K.C., Cropper, W.P., Jr., and Gholz, H.L. 1987. Soil CO₂ evolution in Florida slash pine plantations. I. Changes through time. *Can. J. For. Res.* **17**: 325–329.
- Fan, S.-M., Goulden, M.L., Munger, J.W., Danube, B.C., Bakwin, P.S., Wofsy, S.C., Amthor, J.S., Fitzjarrald, D.R., Moore, K.E., and Moore, T.R. 1995. Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: a growing season of whole-ecosystem exchange measurements by eddy correlation. *Oecologia*, **102**: 443–452.
- Federer, C.A. 1984. Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods. *Can. J. For. Res.* **14**: 763–767.
- Fernandez, I.J., Son, Y., Kraske, C.R., Rustad, L.E., and David, M.B. 1993. Soil carbon dioxide characteristics under different forest types and after harvest. *Soil Sci. Soc. Am. J.* **57**: 1115–1121.
- Gordon, A.M., Schlentner, R.E., and Van Cleve, K. 1987. Seasonal patterns of soil respiration and CO₂ evolution following harvesting in the white spruce forests of interior Alaska. *Can. J. For. Res.* **17**: 304–310.
- 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., and Munger, J.W. 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science (Washington, D.C.)*, **279**: 214–217.
- Ham, J.M., and Knapp, A.K. 1998. Fluxes of CO₂, water vapor, and energy from a prairie ecosystem during the seasonal transition from a carbon sink to a carbon source. *Agric. For. Meteorol.* **89**: 1–14.
- Harmon, M.E., Ferrell, W.K., and Franklin, J.F. 1990. Effects of carbon storage on conversion of old-growth forests to young forests. *Science (Washington, D.C.)*, **247**: 699–702.
- Heath, L.S., Kauppi, P.E., Burschel, P., Gregor, H.-D., Guderian, R., Kohlmaier, G.H., Lorenz, S., Overdieck, D., Scholz, F., Thomasius, H., and Weber, M. 1993. Contribution of temperate forests to the world's carbon budget. *Water Air Soil Pollut.* **70**: 55–69.
- Hollinger, D.Y., Kelliher, F.M., Schulze, D.-E., Bauer, G., Arneth, A., Byers, J.M., Hunt, J.E., McSeveny, T.M., Kobak, K.I., Milukova, I., Sogatchev, A., Tatarinov, F., Varlargin, A., Ziegler, W., and Vygodskaya, N.N. 1998. Forest-atmosphere carbon dioxide exchange in eastern Siberia. *Agric. For. Meteorol.* **90**: 291–306.
- Hollinger, D.Y., Goltz, S.M., Davidson, E.A., Lee, J.T., Tu, K., and Valentine, H.T. 1999. Seasonal patterns and environmental control of carbon dioxide and water vapour exchange in an ecotonal boreal forest. *Global Change Biol.* **5**: 891–902.
- Horst, T.W., and Weil, J.C. 1992. Footprint estimation for scalar flux measurements in the atmospheric surface layer. *Boundary Layer Meteorol.* **59**: 279–296.
- Jarvis, P.G., Massheder, J.M., Hale, S.E., Moncrieff, J.B., Rayment, M., and Scott, S.L. 1997. Seasonal variation of carbon dioxide, water vapor, and energy exchanges of a boreal black spruce forest. *J. Geophys. Res.* **102**: 28 953 – 28 966.
- Johnson, D.W. 1992. Effects of forest management on soil carbon storage. *Water Air Soil Pollut.* **64**: 83–120.
- Kawaguchi, H., and Yoda, K. 1989. Carbon-cycling changes during regeneration of a deciduous broadleaf forest after clear-cutting II. Aboveground net production. *Ecol. Res.* **4**: 271–286.
- Keeling, R.F., Piper, S.C., and Heimann, M. 1996. Global and hemispheric CO₂ sinks deduced from changes in atmospheric O₂ concentration. *Nature (London)*, **381**: 218–221.
- Kolochugina, T.P., and Vinson, T.S. 1993a. Comparison of two methods to assess the carbon budget of forest biomes in the former Soviet Union. *Water Air Soil Pollut.* **70**: 207–221.
- Kolochugina, T.P., and Vinson, T.S. 1993b. Equilibrium analysis of carbon pools and fluxes of forest biomes in the former Soviet Union. *Can. J. For. Res.* **23**: 81–88.
- Kucera, C.L., and Kirkham, D.R. 1971. Soil respiration studies in tallgrass prairie in Missouri. *Ecology*, **52**: 912–915.
- Kurz, W.A., and Apps, M.J. 1994. The carbon budget of Canadian forests: a sensitivity analysis of changes in disturbance regimes, growth rates, and decomposition rates. *Environ. Pollut.* **83**: 55–61.
- Kurz, W.A., Apps, M.J., Comeau, P.G., and Trofymow, J.A. 1996. The carbon budget of British Columbia's forests 1920–1989: preliminary analysis and recommendations for refinements. Canadian Forest Service and B.C. Ministry of Forests, Victoria, B.C. pp. 1–62.
- Levy, P.E., and Jarvis, P.G. 1998. Stem CO₂ fluxes in two sahelian shrub species (*Guiera senegalensis* and *Combretum micranthum*). *Funct. Ecol.* **12**: 107–116.
- Lewis, T. 1998. The effect of deforestation on ground surface temperatures. *Global Planet. Change*, **18**: 1–13.
- Lindroth, A., Grelle, A., and Morén, A.-S. 1998. Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. *Global Change Biol.* **4**: 443–450.
- Lytle, D.E., and Cronan, C.S. 1998. Comparative soil CO₂ evolution, litter decay, and root dynamics in clear-cut and uncut spruce–fir forest. *For. Ecol. Manage.* **103**: 121–128.
- Man, R., and Lieffers, V.J. 1997. Seasonal variations of photosynthetic capacities of white spruce (*Picea glauca*) and jack pine (*Pinus banksiana*) saplings. *Can. J. Bot.* **75**: 1766–1771.
- Meidinger, D., and Pojar, J. 1991. Ecosystems of British Columbia. B.C. Ministry of Forests, Victoria, B.C. pp. 1–330.
- Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B., III, Vorosmarty, C.J., and Schloss, A.L. 1993. Global climate change and terrestrial net primary production. *Nature (London)*, **363**: 234–240.
- Monteith, J.L., and Unsworth, M.H. 1990. Principles of environmental physics. Edward Arnold, New York.
- Moore, T.R. 1983. Winter-time litter decomposition in a subarctic woodland. *Arct. Alp. Res.* **15**: 413–418.
- Norman, J.M., Garcia, R., and Verma, S.B. 1992. Soil surface CO₂ fluxes and the carbon budget of a grassland. *J. Geophys. Res.* **97**: 18 845 – 18 853.
- Olsson, B.A., Staaf, H., Lundkvist, H., Bengtsson, J., and Rosén, K. 1996. Carbon and nitrogen in coniferous forest soils after clear-felling and harvests of different intensity. *For. Ecol. Manage.* **82**: 19–32.
- Pennock, D.J., and van Kessel, C. 1997. Effect of agriculture and clear-cut forest harvest on landscape-scale soil organic carbon storage in Saskatchewan. *Can. J. Soil Sci.* **77**: 211–218.
- Post, W.M., Emanuel, W.R., Zinke, P.J., and Stangenberger, A.G. 1982. Soil carbon pools and world life zones. *Nature (London)*, **298**: 156–159.

- Post, W.M., Peng, T.-H., Emanuel, W.R., King, A.W., Dale, V.H., and DeAngelis, D.L. 1990. The global carbon cycle. *Am. Sci.* **78**: 310–326.
- Price, D.T., and Black, T.A. 1990. Effects of short-term variation in weather on diurnal canopy CO₂ flux and evapotranspiration of a juvenile Douglas-fir stand. *Agric. For. Meteorol.* **50**: 139–158.
- Raich, J.W., and Nadelhoffer, K.J. 1989. Belowground carbon allocation in forest ecosystems: global trends. *Ecology*, **70**: 1346–1354.
- Ryan, M.G., Hubbard, R.M., Clark, D.A., and Sanford, R.L., Jr. 1994. Woody tissue respiration for *Simarouba amara* and *Minquartia guianensis*, two tropical wet forest trees with different growth habits. *Oecologia*, **100**: 213–220.
- Sarmiento, J.L. 1993. Atmospheric CO₂ stalled. *Nature (London)*, **365**: 697–698.
- Schimel, D.S. 1995. Terrestrial ecosystems and the carbon cycle. *Global Change Biol.* **1**: 77–91.
- Sommerfeld, R.A., Mosier, A.R., and Musselman, R.C. 1993. CO₂, CH₄ and N₂O flux through a Wyoming snowpack and implications for global budgets. *Nature (London)*, **361**: 140–142.
- Stannard, D.I. 1997. A theoretically based determination of Bowen-ratio fetch requirements. *Boundary-Layer Meteorol.* **83**: 375–406.
- Striegl, R.G., and Wickland, K.P. 1998. Effects of a clear-cut harvest on soil respiration in a jack pine – lichen woodland. *Can. J. For. Res.* **28**: 534–539.
- Tanner, C.B. 1960. Energy balance approach to evapotranspiration from crops. *Soil Sci. Soc. Am. Proc.* **24**: 1–9.
- Tans, P.P., Fung, I.Y., and Takahashi, T. 1990. Observational constraints on the global atmospheric CO₂ budget. *Science (Washington, D.C.)*, **247**: 1431–1438.
- Turner, D.P., Koerper, G.J., Harmon, M.E., and Lee, J.J. 1995. A carbon budget for forests of the conterminous United States. *Ecol. Appl.* **5**: 421–436.
- Valentini, R., Dore, S., Marchi, G., Mollicone, D., Panfyorov, M., Rebmann, C., Kolle, O., and Schulze, E.-D. 2000. Carbon and water exchanges of two contrasting central Siberia landscape types: regenerating forest and bog. *Funct. Ecol.* **14**: 87–96.
- Verma, S.B., Rosenberg, N.J., and Blad, B.L. 1978. Turbulent exchange coefficients for sensible heat and water vapor under advective conditions. *J. Appl. Meteorol.* **17**: 330–338.
- Waring, R.H., Landsberg, J.J., and Williams, M. 1998. Net primary production of forests: a constant fraction of gross primary production? *Tree Physiol.* **18**: 129–134.
- Watts, W.R., and Neilson, R.E. 1978. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.) VIII. measurements of stomatal conductance and ¹⁴CO₂ uptake in controlled environments. *J. Appl. Ecol.* **15**: 245–255.
- Webb, E.K., Pearman, G.I., and Leuning, R. 1980. Correction of flux measurement for density effects due to heat and water vapour transfer. *Q. J. R. Meteorol. Soc.* **106**: 85–100.
- Weber, M.G. 1990. Forest soil respiration after cutting and burning in immature aspen ecosystems. *For. Ecol. Manage.* **31**: 1–14.
- Woodwell, G.M., Hobbie, J.E., Houghton, R.A., Melillo, J.M., Moore, B., Peterson, B.J., and Shaver, G.R. 1983. Global deforestation: contribution to atmospheric carbon dioxide. *Science (Washington, D.C.)*, **222**: 1081–1086.
- Yarie, J. 1993. Effects of selected forest management practices on environmental parameters related to successional development on the Tanana River floodplain, interior Alaska. *Can. J. For. Res.* **23**: 1001–1014.
- Zinke, P.J., Stangenberger, A.G., Post, W.M., Emanuel, W.R., and Olson, J.S. 1984. Worldwide organic carbon and nitrogen data. Oak Ridge National Laboratory, Oak Ridge, Tenn.