Comparing the carbon budgets of boreal and temperate deciduous forest stands

A.G. Barr, T.J. Griffis, T.A. Black, X. Lee, R.M. Staebler, J.D. Fuentes, Z. Chen, and K. Morgenstern

Abstract: Boreal and temperate deciduous forests at northern mid-latitudes play an important role in the global carbon cycle. We analyze 3 years (1996–1998) of eddy-covariance carbon dioxide flux measurements from two contrasting deciduous forest ecosystems in the boreal and temperate regions of central Canada. The two forest stands have similar ages, heights, and leaf area indices but differ in species composition and climate. Mean annual net ecosystem productivity (NEP) was similar for the two ecosystems, varying between 0.7 and 2.7 t C·ha^{-1} (boreal) and 0.6 and 2.4 t C·ha^{-1} (temperate). In the boreal ecosystem, interannual differences in NEP were primarily controlled by early spring temperature. The warm spring of 1998 caused early leaf out and increased photosynthesis but had little effect on respiration. In the temperate ecosystem, the same warm spring not only caused early leaf out but also increased respiration and drought stress. The contrasting impact of the warm spring on annual NEP at the two sites illustrates the complexity of interpreting climatic impacts on the forest carbon balance. It also illustrates two competing influences of climate change on NEP: spring warming, which promotes photosynthesis and increases NEP, and increased soil temperature and drought, which promote respiration and reduce photosynthesis, thus reducing NEP. We discuss the need for a consistent data post-processing methodology in ecosystem intercomparisons. We also compare our results with a recent synthesis of data from European forests.

Résumé : Les forêts décidues tempérées et boréales situées dans la partie nord des latitudes moyennes jouent un rôle important dans le cycle global du carbone. Nous avons analysé trois années (1996–1998) de mesures de flux de dioxyde de carbone effectuées avec la méthode des corrélations turbulentes dans deux écosystèmes forestiers décidus contrastés des régions tempérées et boréales du centre du Canada. Les deux peuplements forestiers ont un âge, une hauteur et un indice de surface foliaire similaires mais diffèrent par leur composition en espèces et par le climat. La productivité nette annuelle (PNA) des deux écosystèmes était comparable et variait de 0,7 à 2,7 t C·ha^{-1} (boréal) et de 0,6 à 2,4 t C·ha^{-1} (tempéré). Dans l'écosystème boréal, les différences inter-annuelles de PNA étaient surtout contrôlées par la température du début du printemps. Le printemps chaud de 1998 a provoqué un débourrement hâtif et une augmentation de la photosynthèse mais a eu peu d'effet sur la respiration. Dans l'écosystème tempéré, le même printemps chaud n'a pas seulement provoqué un débourrement hâtif mais aussi une augmentation de la respiration et du stress dû à la sécheresse. L'impact différent d'un printemps chaud sur la PNA des deux sites illustre la complexité liée à l'interprétation des impacts climatiques sur le bilan du carbone en forêt. Ce fait illustre aussi deux influences antagonistes d'un changement climatique sur la PNA : un réchauffement printanier favorise la photosynthèse et une augmentation de la PNA, ainsi qu'une augmentation de la température et de la sécheresse du sol qui favorise la respiration et réduit la photosynthèse, réduisant par conséquent la PNA. Nous abordons le besoin d'une méthodologie consistante dans le traitement des données pour comparer les écosystèmes. Nous comparons également nos résultats avec ceux d'une récente synthèse de données provenant de forêts européennes.

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A.G. Barr.[1] Climate Research Branch, Meteorological Service of Canada, 11 Innovation Boulevard, Saskatoon, SK S7N 3H5, Canada.
T.J. Griffis,[2] **T.A. Black, Z. Chen, and K. Morgenstern.** Department of Agricultural Science, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
X. Lee. School of Forestry and Environmental Studies, Yale University, New Haven, CT 06511, U.S.A.
R.M. Staebler.[3] Air Quality Research Branch, Meteorological Service of Canada, Downsview, ON M3H 5T4, Canada.
J.D. Fuentes. Department of Environmental Sciences, University of Virginia, Charlottesville, VA 22903, U.S.A.

[1]Corresponding author (e-mail: alan.barr@ec.gc.ca).
[2]Present address: Department of Soil, Water, and Climate, University of Minnesota, St. Paul, MN 55108, U.S.A.
[3]Present address: Atmospheric Science Research Center, State University of New York, Albany, NY 12203, U.S.A.

Introduction

Boreal and temperate deciduous forests at northern mid-latitudes play an important role in the global carbon cycle (Keeling et al. 1996; Myneni et al. 1997; Fan et al. 1998). Interannual studies have established a strong link between climatic variability and the carbon balance of these ecosystems (Black et al. 2000; Arain et al. 2002; Valentini et al. 2000). These studies indicate that the annual carbon budget of mature northern forests is in near equilibrium and, in some cases, losing carbon to the atmosphere. However, we do not fully understand the processes that govern the carbon budget of northern forest ecosystems, particularly with respect to climatic variability and change. Net ecosystem productivity (NEP), the net exchange of carbon between the ecosystem and the atmosphere, results from the balance between carbon uptake through photosynthesis and carbon release through respiration and decomposition. It is likely that climate change will have a profound effect on NEP in northern ecosystems, because photosynthesis, plant respiration, and soil respiration are each sensitive to temperature and soil moisture (Oechel et al. 1993). It is also likely that northern boreal and northern temperate forests will respond differently because of differences in ecophysiology, nutrient status, the size and quality of the soil carbon pools, and the frequency and intensity of drought.

This study was undertaken to increase our understanding of the processes that control forest NEP and to contrast the responses of boreal and temperate deciduous forest ecosystems to interannual climatic variability. We analyze 3 years of eddy-covariance flux measurements from two deciduous forest stands: a temperate mixedwood stand at Camp Borden, Ontario, and a boreal aspen stand near Prince Albert, Saskatchewan, Canada.

Materials and methods

Sites

This study analyses data from the two long-term, flux-tower sites that have been operated in Canadian deciduous forest ecosystems: Old Aspen (OA) in central Saskatchewan and Camp Borden (CB) in southern Ontario. The OA site was established in 1993 as part of the Boreal Ecosystem–Atmosphere Study (BOREAS; Sellers et al. 1995) and has continued since 1997 as part of the Boreal Ecosystem Research and Monitoring Sites initiative (BERMS; McCaughey et al. 2000). The CB site was established in 1985 as part of Environment Canada's research infrastructure and has had continuous eddy-covariance measurements since July 1995 (Lee et al. 1999; Staebler et al. 2000).

Table 1 compares and contrasts the two sites. The two forest stands have similar ages, heights, and leaf area indices but differ in species composition, climate, and fetch. Both stands are predominantly deciduous; however, OA is dominated by two species in distinct under- and over-storeys, whereas CB has many species in the overstorey and white pine (*Pinus strobus* L.) saplings in a successional understorey. The climate is considerably warmer and wetter at CB than OA. In addition, the OA stand is uniform for at last 3 km in all directions from the flux tower, whereas the CB stand is uniform for between 1.5 and 4 km to the south

(from 90 to 255°, using north as 0°) but has inadequate fetch to the north (from 255 to 90°; Lee et al. 1999).

Climate measurements

Both sites have a complete regimen of climate measurements (Staebler et al. 2000; McCaughey et al. 2000). Here we mention only those measurements that are used in this study. Photosynthetically active radiation (Q_p) was measured using LI-COR LI-190SA quantum sensors mounted at the top of the flux towers. Air temperature (T_a) was measured at 37 m at OA using a Vaisala HMP35 temperature/humidity sensor in an unventilated Gill shield and at 33 m at CB using a ventilated copper–constantan thermocouple. Soil temperature (T_s) was measured at 0.05-m depth using chromel–constantan thermocouples at OA and precision thermistors at CB. Precipitation (P) was measured year round at OA in a forest clearing using an accumulating gauge (Belfort 5915 with an Alter shield) with motor oil added to prevent water losses by evaporation. Precipitation was not measured at CB; we used data from the nearest gauge at Egbert, Ont., 15 km to the SE of the flux tower. At this distance from CB, the half-hourly or daily precipitation data may not represent the forest stand at the flux tower but the seasonal and annual cycles should be representative.

Flux measurements

Half-hourly fluxes of carbon dioxide, water vapour (E) or latent heat (λE), and sensible heat (H) were measured using the eddy-covariance technique beginning on 1 April 1996 (OA) and 15 July 1995 (CB). (The fluxes were also measured between 2 February and 19 September 1994 at OA.) At both sites, the eddy-covariance system consisted of a tri-axial sonic anemometer (Gill Instruments Solent R2 or R3 at OA and Kaijo Denki DAT-310 at CB) in combination with a closed-path infrared gas analyzer (LI-6262; LI-COR, Inc., Lincoln, Nebr.) operated in differential mode. Chen et al. (1999) and Staebler et al. (2000) provide additional measurement details. The flux measurements at CB were rejected when the wind was from the north (between 255° and 90°), where fetch was inadequate. This represented 41% of the data.

The carbon dioxide (CO_2) flux is a direct measure of NEP, which in turn is the difference between gross ecosystem photosynthesis (GEP) and ecosystem respiration (ER):

[1]   NEP = GEP – ER

Positive NEP (downward CO_2 flux) indicates that the ecosystem is a CO_2 sink. At night, NEP equals ER and GEP is zero. During the day, we partitioned NEP between ER and GEP by first estimating ER from eq. 2 below and then calculating GEP from eq. 1.

Flux corrections and gap filling

The CO_2 flux (NEP) was corrected for underestimation by eddy covariance by adjusting for energy-balance closure and rejecting low wind speed fluxes at night. During the day and during periods with high wind speeds at night, we assumed that eddy covariance underestimated the CO_2 flux by the same fraction that it underestimated the sensible and latent heat fluxes (Black et al. 2000; Twine et al. 2000). The energy-closure adjustment factor was estimated by compar-

Table 1. Site characteristics.

Site	Camp Borden (CB)	Old Aspen (OA)
Latitude (°N)	44.32	53.63
Longitude (°W)	79.93	106.20
Elevation (m)	120	601
Mean annual temperature (°C)	6.4	0.5
Mean annual precipitation (mm)	858	406
Soil texture	Loamy sand	Loam to clay loam
Ecosystem type	Temperate mixed wood	Boreal deciduous
Overstorey species	Red maple (*Acer rubrum* L.), trembling aspen (*Populus tremuloides* Michx.), white ash (*Fraxinus americana* L.), large-tooth aspen (*Populus grandidentata* Michx.), black cherry (*Prunus serotina* Ehrh.)	Trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.)
Understorey species	Eastern white pine (*Pinus strobus* L.)	Beaked hazel (*Corylus cornuta* Marsh.)
Stand age (years)	90	70
Leaf area index	4.1	2.5 (overstorey), 2.0 (understorey)
Canopy height (m)	22	21
Eddy correlation height (m)	33	39
Fetch	1.5 to 4 km to the south (between 90 and 255°, using north as 0°), inadequate (0.5–1.5 km) in other directions.	3 km in all directions

Note: Mean values for annual temperature and precipitation were calculated using 1961–1990 normals from the nearest climate station: Prince Albert Airport (53°13′N, 105°41′W, 428 m elevation) for OA and Essa (44°22′N, 79°48′W, 216 m elevation) for CB (Meteorological Service of Canada 2001).

Fig. 1. Sensitivity of mean annual net ecosystem productivity (NEP, t C·ha^{-1}) and ecosystem respiration (ER, t C·ha^{-1}) to variations in the u_* threshold (u_*^{TH}) used to reject nighttime CO_2 fluxes.
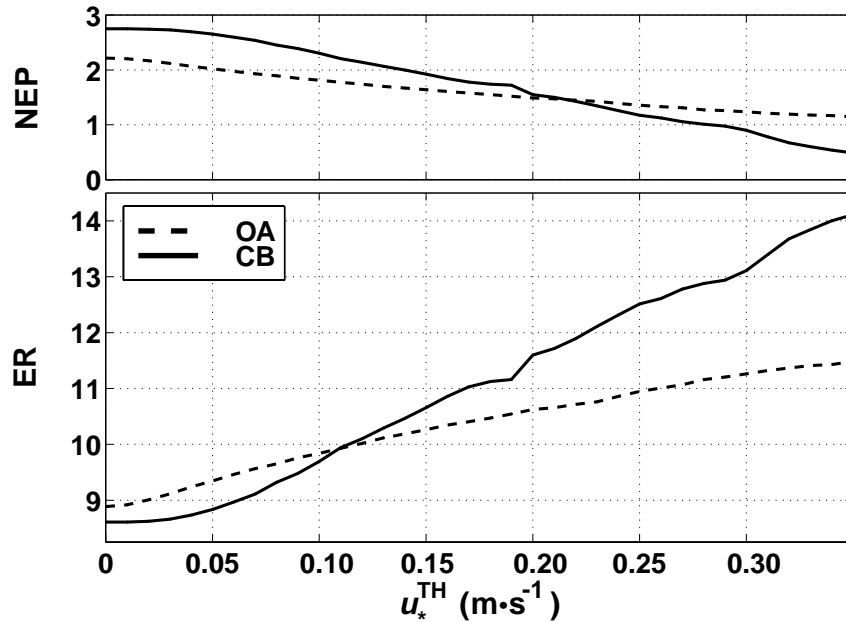
ing the sum $H + \lambda E$ with surface available energy (net radiation minus the sum of the minor surface energy balance terms). We used an adjustment factor of 12.5% at both sites based on the 1996–1998 data at OA and the earlier analysis of Barr et al. (1994) at CB.

At night, we corrected the CO_2 flux by (*i*) applying the 12.5% energy-closure adjustment to high wind speed fluxes (i.e., with $u_* \geq u_*^{TH}$, where u_* is the friction velocity as measured by eddy covariance and u_*^{TH} is a threshold below which measured nighttime fluxes are rejected (Goulden et al.

1996*a*)) and (*ii*) replacing low wind-speed ($u_* < u_*^{TH}$) fluxes with values estimated from the following empirical relationship between the closure-adjusted, high wind speed fluxes, and soil temperature at 0.05 m (Black et al. 2000):

[2] $$\text{NEP} = \text{ER} = \frac{a_1}{1 + e^{a_2(a_3 - T_s)}}$$

Equation 2 was also used to fill gaps in NEP at night and to estimate ER during the day.

Fig. 2. Annual cycles of air temperature (37 m at OA and 33 m at CB), soil temperature (0.05 m), and precipitation minus evapotranspiration. The temperatures are plotted as 28-day means. The 1961–1990 normals in the air temperature plots are from the nearest climate station: Prince Albert Airport (53°13′N, 105°41′W, 428 m elevation) for OA and Essa (44°22′N, 79°48′W, 216 m elevation) for CB (Meteorological Service of Canada 2001).
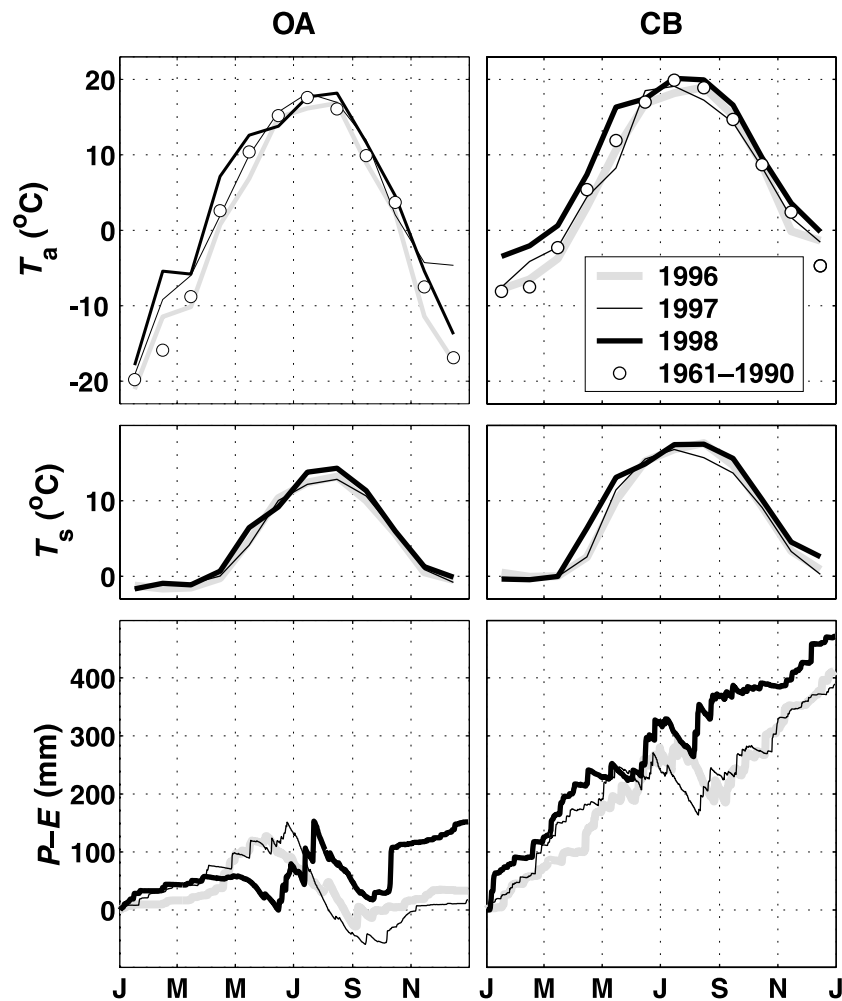
During the day, gaps in NEP were filled using the following empirical relationship between measured (closure-adjusted) NEP and photosynthetically active radiation (Lee et al. 1999):

$$[3] \qquad \text{NEP} = b_0 + b_1 \left(\frac{Q_p}{b_2 + Q_p} \right)$$

The value for b_2 in eq. 3 was held constant, whereas b_0 and b_1 were allowed to vary in time. We first estimated b_2 (700 μmol·m^{-2}·s^{-1} at OA and 820 μmol·m^{-2}·s^{-1} at CB) using all daytime data from the fully leafed period, then estimated b_0 and b_1 every 5 days using a 15-day moving window.

Priestley–Taylor alpha

The Priestley–Taylor coefficient α (Priestley and Taylor 1972) was estimated as

$$[4] \qquad \alpha = \frac{(s + \gamma)\lambda E}{s(H + \lambda E)}$$

where γ is the psychrometric constant and s is the derivative of saturation vapor pressure with respect to temperature. $H + \lambda E$ has been substituted for $R_n - Q$ in Priestley and Taylor's original formulation, where Q is the sum of the minor energy balance terms, to avoid the issue of energy-balance nonclosure. The substitution of $H + \lambda E$ for $R_n - Q$ in eq. 4 has the same effect on α as adjusting H and λE to force energy-balance closure.

Results

Effect of flux corrections on NEP, ER, and GEP

The components of the annual carbon balance were sensitive to the flux correction and gap-filling schemes as shown in Fig. 1 and Table 2. We varied two features in the correction scheme: the u_* threshold (u_*^{TH}) used to reject bad nighttime CO_2 fluxes and the use or nonuse of the energy-closure adjustment. Figure 1 shows the sensitivity of mean annual NEP and ER to u_*^{TH}. The response is complex because of different responses day and night and different responses between OA and CB. Increasing u_*^{TH} (*i*) increased ER by elim-

Table 2. Influence of u_*^{TH} (the threshold used to reject low wind speed data at night) and the use or nonuse of an energy-closure adjustment on the annual carbon balance (in t C·ha^{-1}).

	u_*^{TH} (m·s^{-1})	Energy closure	OA			CB		
			1996	1997	1998	1996	1997	1998
NEP	0.15	No	0.8	1.2	2.5	0.9	2.4	1.9
	0.35	No	0.4	0.8	2.0	–0.4	1.2	0.6
	0.35	Yes	0.4	0.9	2.3	–0.4	1.4	0.7
ER	0.15	No	9.0	9.0	9.3	9.2	8.9	10.0
	0.35	No	9.9	10.1	10.5	12.0	11.5	12.9
	0.35	Yes	11.2	11.3	11.8	13.4	12.9	14.6
GEP	0.15	No	9.7	10.2	11.8	10.1	11.4	11.9
	0.35	No	10.3	10.8	12.5	11.6	12.7	13.6
	0.35	Yes	11.6	12.2	14.1	13.0	14.3	15.3

Table 3. Annual carbon balance (in t C·ha^{-1}), estimated using a value for u_*^{TH} of 0.20 m·s^{-1} and an energy-closure adjustment.

	OA				CB			
	1996	1997	1998	Mean±SD	1996	1997	1998	Mean±SD
NEP	0.7	1.2	2.7	1.5±1.0	0.6	2.4	1.7	1.5±0.9
ER	10.5	10.5	10.9	10.6±0.2	11.4	11.0	12.4	11.6±0.7
GEP	11.2	11.7	13.5	12.1±1.2	12.0	13.3	14.1	13.1±1.1

inating low nighttime values of ER and increasing the daytime estimates of ER from eq. 2, (*ii*) increased GEP during the day by the same amount as ER but not at night when GEP was zero, and (*iii*) reduced NEP at night but not during the day. The resultant, negative impact of increasing u_*^{TH} on NEP was smaller than the associated positive impact on ER.

Somewhat surprisingly, the impact of u_*^{TH} on NEP and ER also differed significantly between sites. The impact was larger at CB than OA, because the coefficients in eq. 2 were more sensitive to u_*^{TH} at CB. The resulting ER estimates from CB and OA were similar at low u_*^{TH} but diverged at high u_*^{TH}. For example, increasing u_*^{TH} from 0.15 to 0.35 m·s^{-1} increased mean annual ER from 9.4 to 12.1 t C·ha^{-1} at CB compared with 9.1 to 10.2 t C·ha^{-1} at OA. The corresponding declines in mean annual NEP were –1.3 t C·ha^{-1} at CB compared with –0.4 t C·ha^{-1} at OA. Because NEP and ER did not approach an asymptote as u_*^{TH} increased, we were not able to identify a preferred value for u_*^{TH} from this analysis. Fortunately for climatic impact studies, u_*^{TH} had a much smaller impact on interannual differences in NEP than on the absolute magnitude of NEP.

The higher sensitivity of NEP and ER to u_*^{TH} at CB may be related to sample size; at CB, data were rejected from wind sectors with inadequate fetch. It may also reflect unique site characteristics at CB. The CB forest stand is a 5 km wide island of forest in a sea of crop- and grass-land, and the flux measurement at CB is made near the forest's northern edge. We do not know how these features influence the mesoscale circulations at the flux tower or what the consequent impact is on the eddy-covariance measurements.

The second data correction (the use or nonuse of an energy-closure adjustment) had a smaller influence than u_*^{TH} on NEP. Although the energy-closure adjustment caused large changes in ER and GEP, the changes were opposite in sign so that net impact on NEP was small.

Table 3 gives our "best" estimates for NEP, ER, and GEP, made using the energy-closure adjustment and a value for u_*^{TH} of 0.20 m·s^{-1}. Based on these adjustments, the sites show identical mean annual NEP of 1.5 t C·ha^{-1}, with mean annual ER and GEP at CB both exceeding the values at OA by 1.0 t C·ha^{-1}.

Seasonal cycles of NEP, ER, and GEP

Figure 2 shows the interannual differences in air temperature, soil temperature, and cumulative precipitation minus evapotranspiration at OA and CB. At both OA and CB, the primary interannual climatic differences were in early spring air and soil temperatures. April–May 1998 was unusually warm. All 3 years were relatively wet, and although we believe that soil moisture stress can be important at both sites and at CB in particular, none of the years in this study had periods of severe growing-season drought.

Figure 3 shows interannual variability in the seasonal cycles of NEP, ER, GEP, and the daytime Priestley–Taylor coefficient α. The most striking features in the seasonal cycle of GEP are the early timing of the spring rise in GEP in 1998 at both sites, the contrast between OA and CB in the shape of the spring rise in GEP, and the atypically low value for fully leafed GEP at CB during late May and June 1998. The early spring rise of GEP in 1998 at both sites reflects the warm spring and early leaf out of 1998 (Black et al. 2000; Barr et al. 2000). The spring rise in GEP occurred in two distinct phases at CB but only one phase at OA. The two-phase rise in GEP at CB reflects the mixed coniferous and deciduous species composition, with the earlier, conifer phase (from 0 to ~1 g C·m^{-2}·day^{-1}) occurring after thaw and

Fig. 3. Annual cycles of NEP, ER, GEP (all in g C·m^{-2}·day^{-1}), and the Priestley–Taylor coefficient α. The values are 5-day means. NEP, ER, and GEP were corrected using a value for u_*^{TH} of 0.20 m·s^{-1} and an energy-closure adjustment of 12.5%. The 5-day mean values for α were estimated from 5-day mean fluxes for periods with $Q_p > 500$ μmol·m^{-2}·s^{-1}.
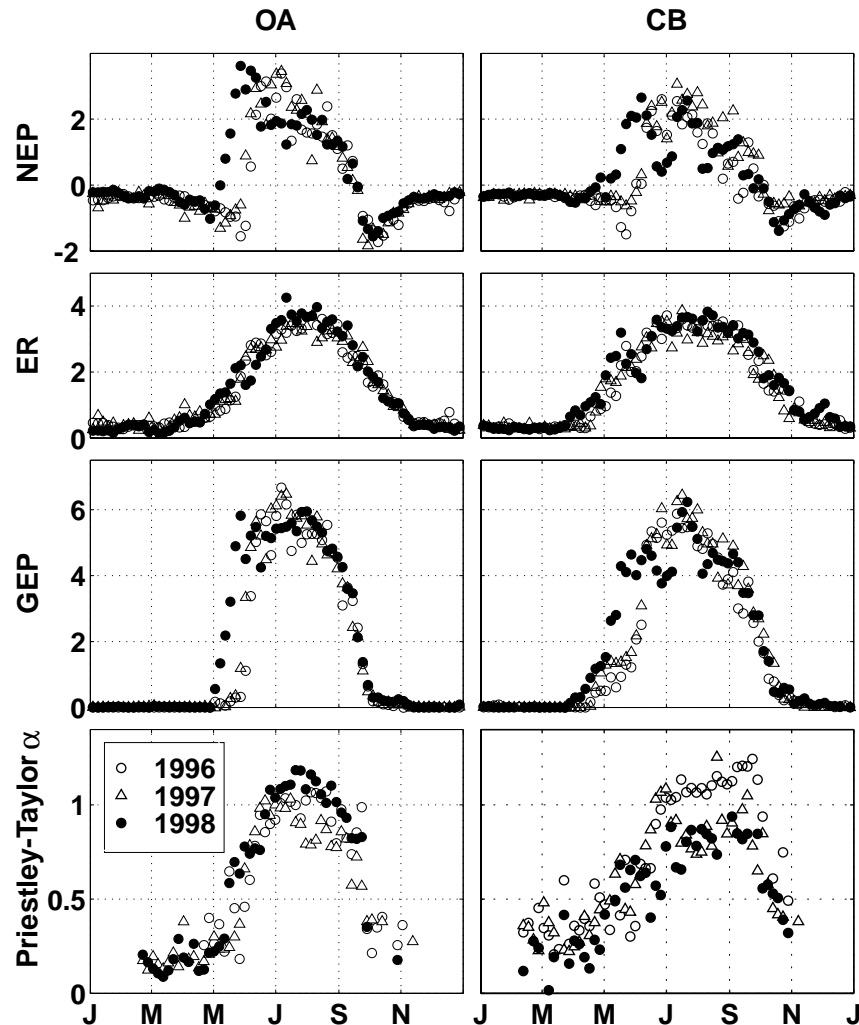
before leaf out and the later phase (from 1 to ~5 g C·m^{-2}·day^{-1}) corresponding to leaf out. The depression in GEP and α in May–June 1998 at CB may indicate drought stress. A similar but smaller depression also occurred during May–June 1998 at OA. Although we lack a complete profile of soil moisture data at CB to verify that, in fact, the depression in GEP was caused by drought stress, the occurrence of drought is supported by the concurrently low value for α. Cumulative precipitation minus evapotranspiration (Fig. 2) also supports the possibility of drought stress in May–June 1998 at CB; however, the analysis is not definitive, because CB precipitation was not measured on site.

The seasonal cycles of NEP, ER, and GEP each show a longer growing season at CB than OA associated with the temperate versus boreal climatic contrast and with the differences in species composition. The spring transition is more gradual at CB than OA, because the conifers at CB began to photosynthesize well before the deciduous species leafed out, albeit at much lower rates. At both sites, the seasonal cycles of ER and GEP are nearly symmetric, but ER lags GEP by about 1 month and the spring-to-autumn rise and fall extends over a longer period for ER than GEP. The

lag and extension of ER relative to GEP lead to a pronounced asymmetry in the seasonal cycle of NEP, with a very sharp rise in spring. They also produce two distinct shoulder seasons, most pronounced in autumn, when the ecosystem is a strong source of carbon to the atmosphere. Seasonal asymmetry in NEP appears to be a general feature of northern deciduous ecosystems (Chen et al. 1999). The seasonal cycle of ER shows much less interannual variability than GEP, although there is a subtle indication that the depression in GEP during May–June 1998 at CB is accompanied by a depression in ER.

Interannual variability and climatic controls on NEP

Both sites show large interannual variability in NEP (Figs. 3 and 4), but the causes of the variability are different. At OA, the warm spring and early leaf out of 1998 caused a large increase in GEP but had little effect on ER so that net annual NEP in 1998 was the highest of the 3 years. At CB, this same warm spring caused a large increase in GEP, particularly in May. However, the net GEP increase in 1998 was smaller at CB than OA. Early summer GEP at CB was in fact lowest in 1998, apparently because of drought stress in

Fig. 4. Cumulative NEP, ER, and GEP (all in t C·ha^{-1}) from Fig. 3.
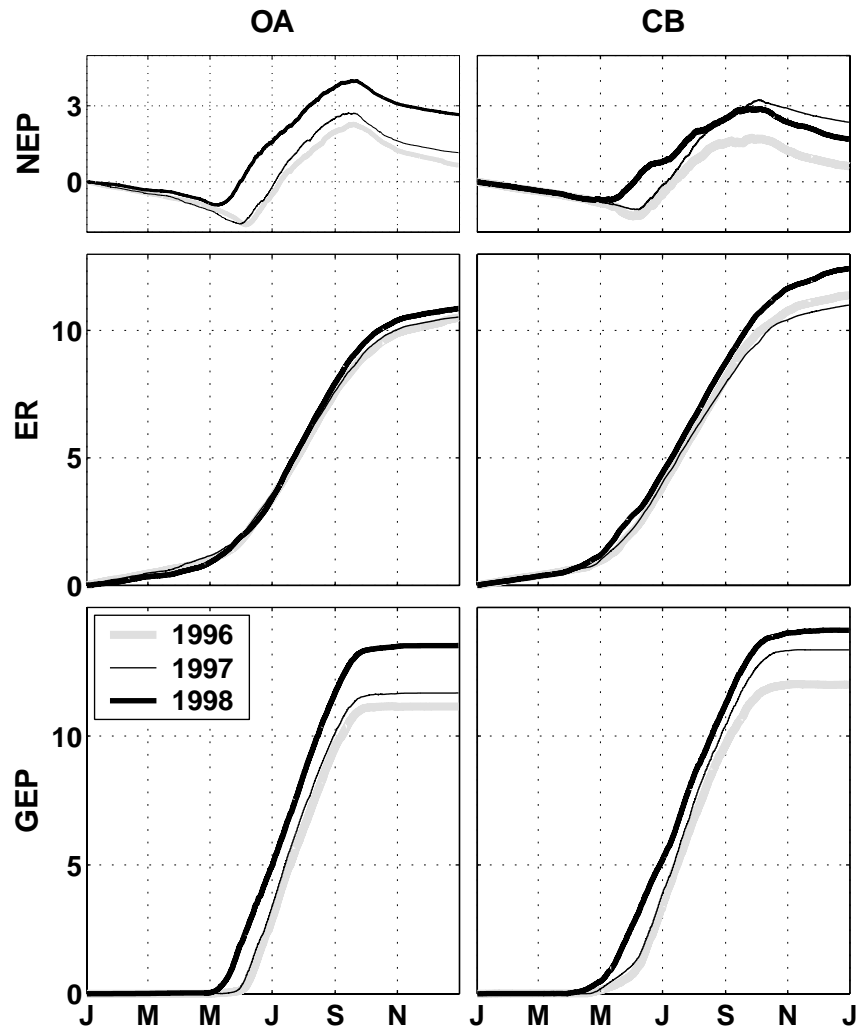
May and June. In addition, the warm spring and autumn of 1998 also caused a moderate increase in ER at CB. The increased respiration and drought stress at CB in 1998 resulted in a net annual NEP that is intermediate between 1996 and 1997 despite the large increase in spring GEP.

Ecosystem respiration appears to be largely controlled by soil temperature at both sites (Fig. 5). The interannual differences in ER match the interannual differences in T_s, although any inferences that are drawn from the annual ER values in this study must be tempered by the realization that the annual values include daytime and gap-filled values of ER that were modeled as a function of T_s (eq. 2). The increase in both ER and T_s in 1998 is larger at CB than OA despite the large increase in spring air temperature at both sites. On average, ER is slightly larger at CB than OA. However, for a given value of T_s, ER is ~30% higher at OA than CB (Fig. 5). The difference between sites in Fig. 5 is striking and may indicate that the soil carbon pool is smaller or less labile at CB than OA. Plans are underway to collect the necessary data to confirm this. The overall result is that despite the much higher soil temperature and longer period when the soil is thawed at CB, mean annual ER is only slightly larger at CB than OA.

Discussion

Importance of flux corrections

The sensitivity of NEP to the data-correction and gap-filling methodology demonstrates the need to adopt a common post-processing methodology before comparing NEP among sites and ecosystems (Falge et al. 2001). In this study, the relevant components of the post-processing methodology are the use of $u_*^{TH} = 0.20$ m·s^{-1} to reject low wind speed fluxes at night, the use of an energy-closure adjustment, the rejection of data from wind sectors with inadequate fetch (at CB), and the use of empirical relationships in eqs. 2 and 3 to estimate ER during the day and to fill gaps in ER and NEP. At other sites, other components may also be important, including spectral corrections and other types of filtering (see, e.g., Massman 2000). The relative importance of the post-processing components will undoubtedly vary among sites because of the unique features and issues of each site, such as fetch limitations, topographical challenges, discontinuities in roughness, spatial heterogeneity, and local and mesoscale atmospheric circulations.

Previously published results from OA and CB used slightly different adjustment schemes. Black et al. (2000)

Fig. 5. The influence of soil temperature at 0.05 m on ER, for
30-min values (main plot) and annual values (insert). ER was
corrected as in Fig. 3. The 30-min values are means, binned by
T_s class, of measured values only (i.e., without gap filling) from
1996 to 1998. The lines (ER = $0.47/(1 + e^{0.21(10.9-T_s)})$, $r^2 = 0.99$
at OA and ER = $0.41/(1 + e^{0.21(12.9-T_s)})$, $r^2 = 0.99$ at CB) were fit
by least-squares nonlinear regression.
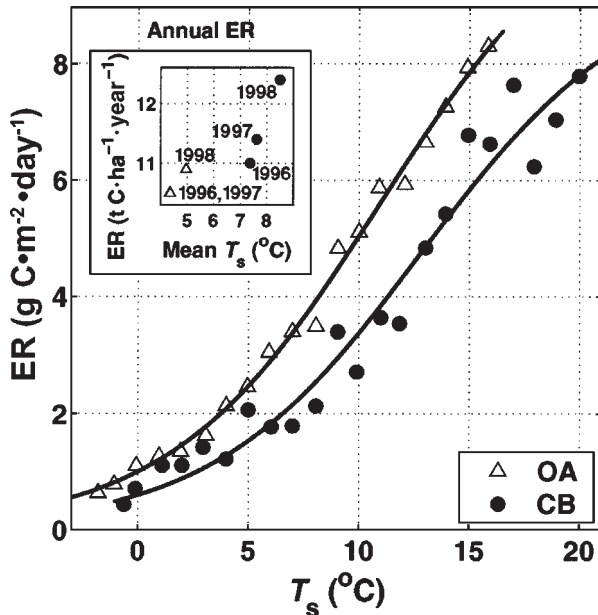
used u_*^{TH} of 0.35 m·s^{-1} and applied an energy-closure adjust-
ment at OA, whereas Lee et al. (1999) used u_*^{TH} of 0.15 m·s^{-1}
with no energy-closure adjustment at CB. While these dif-
ferences do not affect the main conclusions of these studies,
concerning the influence of interannual climatic variability
on NEP, they do limit our subsequent ability to compare
NEP between sites. Care should be exercised in comparing
NEP between sites, with due attention given to the post-
processing details. In a comprehensive study of gap-filling
strategies for eddy-covariance data, Falge et al. (2001)
showed that the effect of different gap-filling strategies on
annual NEP was comparable with the value for annual NEP
itself.

In this study, the post-processing scheme had a large im-
pact on the absolute magnitude of NEP but did not affect
interannual differences in NEP. The inference is that we can
place greater confidence in the interannual differences in
NEP than in the mean annual value for NEP. We believe that
this inference applies broadly to eddy-covariance studies.
For northern ecosystems that are in near equilibrium with re-
spect to carbon exchange, the resulting uncertainty in NEP
will make it difficult to ascertain whether individual ecosys-
tems are in fact weak sinks or weak sources of carbon to the
atmosphere. Still, the uncertainties in annual NEP from the
eddy-covariance method are much smaller than from any
other method.

Climatic controls on NEP and ER

The contrasting responses of NEP to interannual climatic
differences at OA and CB illustrate the complexity of inter-
preting the impacts of climate change on NEP in northern

forest ecosystems. Climate change may bring competing
influences on NEP. Warmer springs enhance GEP by length-
ening the growing season and increasing nutrient mineraliza-
tion (Black et al. 2000; Jarvis and Linder 2000). Increased
stress from drought and high temperatures during the grow-
ing season reduces GEP. Warmer soils and a longer period
when the soil is not frozen enhance ER (Goulden et al.
1998). The resultant impact on NEP, which is the difference
between GEP and ER, is complex and will be difficult to
predict.

The contrasting responses of OA and CB to the warm
spring of 1998 highlight two recent debates in the carbon
budget literature concerning the sensitivity of NEP and ER
to climatic variability and the relative importance of ER in
the carbon balance of northern forests. Studies of northern
terrestrial ecosystems by Black et al. (2000) and Griffis et al.
(2001) show that ER is a relatively conservative component
of the carbon balance. However, in a recent, landmark analy-
sis, Valentini et al. (2000) reported that ER is the main de-
terminant of the carbon balance in European forests.
Valentini's analysis suggests that annual forest GEP in Eu-
rope is nearly constant across a broad latitudinal band so
that the north–south gradient in NEP is controlled almost en-
tirely by the gradient in ER.

The corollary of Valentini's analysis is that climate exerts
its primary influence on NEP via respiration, not photosyn-
thesis. This conclusion is both surprising and controversial
(Grace and Rayment 2000; Janssens et al. 2001; Piovesan
and Adams 2001). The mean GEP from OA and CB (Ta-
ble 3) are similar to each other and fall well within the range
reported by Valentini et al. They support Valentini's conclu-
sion that GEP is nearly constant with latitude above 40°N.
However, other results from OA and CB are not fully consis-
tent with Valentini's conclusions. Firstly, the annual values
of GEP from OA and CB show large interannual differences
that are clearly influenced by climate. Moreover, the
interannual differences in NEP and GEP exceed the
interannual differences in ER at both OA and CB, so that
climate appears to have greater influence on GEP than ER.
Interannual climatic differences may in fact be useful as
proxies of climate change or of climatic gradients in space
with one limitation: they reflect only short time scales and
do not account for long-term acclimation to temperature
change (see the discussion below).

Secondly, whereas Valentini's latitudinal analysis predicts
a difference in the OA and CB NEP/ER ratios of ~0.5 (0.2
for OA versus 0.7 for CB), the measured NEP/ER ratios are
nearly identical (0.14 for OA and 0.13 for CB). Compared
with other low-latitude sites in Valentini's study, CB is a def-
inite outlier, with lower NEP and higher ER. However, CB
has a much more continental climate than any of the Euro-
pean sites at similar latitudes. We would argue that whereas
latitude integrates the main features of climate within Eu-
rope and thus serves as a good independent variable for eco-
system intercomparisons within Europe, its use breaks down
when sites are added from outside Europe. In this case, it is
more appropriate to compare sites of similar climate than
similar latitude. If we adopt this approach and compare CB
with the European sites of similar temperature and precipita-
tion, such as the German forests at 50°N or the forests in
Belgium, Sweden, or Finland (Valentini et al. 2000), the

NEP/ER ratio at CB falls well within the European range. It is also comparable with the values for two temperate deciduous forests in the northern United States (0.23 (Goulden et al. 1996b) and 0.22 (Schmid et al. 2000)). It is then OA that stands out, with a climate that is colder and lower in precipitation than any of the European sites in Valentini et al. (2000).

Two issues may in part explain the differences between studies: acclimation versus persistence and differences in the responses of photosynthesis, heterotrophic respiration, and autotrophic respiration to climate. Giardina and Ryan (2000) reported that the heterotrophic component of ER is insensitive to temperature over decadal time scales because of the rapid decomposition and, thus, limited availability of labile substrate. Thus, heterotrophic respiration may be substrate limited. This conclusion is supported by Janssens et al. (2001), who analyzed soil and ecosystem respiration from the same European forests as in Valentini et al. (2000) and concluded that differences in respiration across European forests are controlled, not primarily by temperature, but by GEP. They found that temperature controls interannual differences in ER within sites but not geographic differences in ER among sites. Giardina and Ryan's conclusion that heterotrophic respiration is insensitive to temperature is also supported by the soil warming experiments of Jarvis and Linder (2000), who found an almost complete acclimation of soil respiration within 5 years of the initiation of soil warming. In contrast, there is evidence that the autotrophic component of ER, which can account for more than 50% of GEP (Ryan et al. 1997), does not always acclimate to temperature change. Acclimation has been observed in some species, e.g., black spruce (*Picea mariana* (Mill.) BSP) and trembling aspen (*Populus tremuloides* Michx.) (Tjoelker et al. 1999), but not others, e.g., white spruce (*Picea glauca* (Moench) Voss) (Weger and Guy 1991). The speed of acclimation may also differ among ecosystems. Rapid acclimation should result in near-perfect homeostasis and minimal CO_2 release but annual losses may be substantial if acclimation is slow (Atkin et al. 2000).

The issues that influence NEP are clearly complex and merit further study. Warmer temperatures and drier soil conditions may impact ER and GEP differently. They may also impact growth and maintenance respiration versus soil microbial respiration differently. To resolve these questions, studies of forest–atmosphere CO_2 exchange are needed over much longer time scales than the 3 years in this study and additional measurements are needed to partition ER into its auto- and hetero-trophic components.

Acknowledgements

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