

# Climatic controls on the carbon and water balances of a boreal aspen forest, 1994–2003

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## Abstract

The carbon and water budgets of boreal and temperate broadleaf forests are sensitive to interannual climatic variability and are likely to respond to climate change. This study analyses 9 years of eddy-covariance data from the Boreal Ecosystem Research and Monitoring Sites (BERMS) Southern Old Aspen site in central Saskatchewan, Canada and characterizes the primary climatic controls on evapotranspiration, net ecosystem production ( $F_{NEP}$ ), gross ecosystem photosynthesis ( $P$ ) and ecosystem respiration ( $R$ ). The study period was dominated by two climatic extremes: extreme warm and cool springs, which produced marked contrasts in the canopy duration, and a severe, 3-year drought.

Annual  $F_{NEP}$  varied among years from 55 to 367 g C m<sup>-2</sup> (mean 172, SD 94). Interannual variability in  $F_{NEP}$  was controlled primarily by factors that affected the  $R/P$  ratio, which varied between 0.74 and 0.96 (mean 0.87, SD 0.06). Canopy duration enhanced  $P$  and  $F_{NEP}$  with no apparent effect on  $R$ . The fraction of annual photosynthetically active radiation (PAR) that was absorbed by the canopy foliage varied from 38% in late leaf-emergence years to 51% in early leaf-emergence years. Photosynthetic light-use efficiency (mean 0.0275, SD 0.026 mol C mol<sup>-1</sup> photons) was relatively constant during nondrought years but declined with drought intensity to a minimum of 0.0228 mol C mol<sup>-1</sup> photons during the most severe drought year. The impact of drought on  $F_{NEP}$  varied with drought intensity. Years of mild-to-moderate drought suppressed  $R$  while having little effect on  $P$ , so that  $F_{NEP}$  was enhanced. Years of severe drought suppressed both  $R$  and  $P$ , causing either little change or a subtle reduction in  $F_{NEP}$ . The analysis produced new insights into the dominance of canopy duration as the most important biophysical control on  $F_{NEP}$ .

The results suggested a simple conceptual model for annual  $F_{NEP}$  in boreal deciduous forests. When water is not limiting, annual  $P$  is controlled by canopy duration via its influence on absorbed PAR at constant light-use efficiency. Water stress suppresses  $P$ , by reducing light-use efficiency, and  $R$ , by limiting growth and/or suppressing microbial respiration. The high photosynthetic light-use efficiency showed this site to be a highly productive boreal deciduous forest, with properties similar to many temperate deciduous forests.

**Keywords:** boreal deciduous forest, canopy duration, carbon balance, drought, ecosystem respiration, evapotranspiration, gross ecosystem photosynthesis, net ecosystem production, soil water, water balance

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## Introduction

The data from flux-tower studies, many of which began in the early-to-mid 1990s, are just now becoming long

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enough to allow a thorough analysis of the broad spectrum of climatic and biophysical factors that control the carbon, water and energy cycles of terrestrial ecosystems. Flux towers provide the only viable method to measure the exchanges of carbon, water and energy between ecosystems and the atmosphere over short time scales (i.e. minutes to months), thus enabling the evaluation of seasonal and interannual variability in these exchanges and the elucidation of their climatic controls (Baldocchi *et al.*, 2001). Integrated, stand-level data sets from flux towers are important for: the identification and characterization of key ecophysiological processes in the terrestrial carbon and water cycles (Goulden *et al.*, 1998; Black *et al.*, 2000; Barr *et al.*, 2004); the development and testing of ecosystem process models (Baldocchi & Meyers, 1998; Grant *et al.*, 2005); and the validation of model parameterizations at the stand level (Grant *et al.*, 1999; Law *et al.*, 2000; Amthor *et al.*, 2001; Wilson *et al.*, 2001).

Flux towers have been in long-term operation in several mature forest ecosystems, including the Takayama temperate deciduous forest (Yamamoto *et al.*, 1999; Saigusa *et al.*, 2002), the Harvard temperate deciduous forest (Goulden *et al.*, 1996; Barford *et al.*, 2001), the Walker Branch temperate deciduous forest (Greco & Baldocchi, 1996), the Campbell River Douglas-fir forest (Morgenstern *et al.*, 2004), the Camp Borden temperate mixed-deciduous forest (Lee *et al.*, 1999; Barr *et al.*, 2002), the Howland boreal transitional red spruce forest (Hollinger *et al.*, 1999), the BOREAS Northern Old Black Spruce site (Goulden *et al.*, 1998) and the BOREAS/BERMS Southern Old Aspen (SOA) site (Black *et al.*, 2000; Barr *et al.*, 2004). These sites show significant interannual variability in net ecosystem production ( $F_{NEP}$ ), resulting from the differential effects of climatic variability on gross ecosystem photosynthesis ( $P$ ) and ecosystem respiration ( $R$ ) (Goulden *et al.*, 1996; Yamamoto *et al.*, 1999; Black *et al.*, 2000; Wilson *et al.*, 2000b; Arain *et al.*, 2002; Griffis *et al.*, 2003; Barr *et al.*, 2004). Statistical methods have been used to partition seasonal and interannual variability in weekly  $F_{NEP}$  and  $R$  between external (climatic) controls and internal controls (changes in photosynthetic and respiration relationships) (Hui *et al.*, 2003). At the Duke Forest, the primary source of variability in weekly mean  $F_{NEP}$  and  $R$  was seasonal climatic variability, with interannual climatic variability and seasonal variability in biophysical parameters playing secondary roles.

One of the strengths of comprehensive, long-term datasets is the ability to evaluate potential biophysical feedbacks to climate change. The response of annual  $F_{NEP}$  to climatic variability is complex (Barr *et al.*, 2002), in part because  $F_{NEP}$  integrates three processes, gross ecosystem photosynthesis, autotrophic respiration  $R_a$

and heterotrophic respiration  $R_h$ , all of which respond uniquely. There is evidence that the ratio of  $R_a/P$  is a conservative parameter (Landsberg & Waring, 1997; Waring *et al.*, 1998) that depends on the allocation of carbohydrates to protein synthesis (Dewar *et al.*, 1999) but this hypothesis remains uncertain (Ryan *et al.*, 1997). Some responses to climatic variability are immediate and direct, such as the response of  $P$  to light, temperature and soil water. Others are indirect, mediated through associated biophysical factors, such as leaf phenology (e.g. the effect of spring temperature on the timing of leaf emergence, Black *et al.*, 2000; Barr *et al.*, 2004) and canopy structure (e.g. the reduction in leaf area index (LAI) following drought; Le Dantec *et al.*, 2000). Others are transient, such as the response of  $R$  to warming in northern ecosystems (Jarvis & Linder, 2000). Transient responses that involve physiological adaptation, such as the acclimation of photosynthesis to temperature (Tjoelker *et al.*, 1999), or transient responses that involve temporal changes in site characteristics, such as available soil nitrogen (Jarvis & Linder, 2000) or the labile carbon pool (Giardina & Ryan, 2000; Eliasson *et al.*, 2005; Knorr *et al.*, 2005) are complex and may be challenging to model.

This study analyses 9 years of measurements from the SOA tower-flux site in central Saskatchewan, Canada (1994 and 1996–2003). The SOA site was established in 1993, as a part of the Boreal Ecosystem-Atmosphere Study (BOREAS, Sellers *et al.*, 1997), and has continued since 1997, under the Canadian Boreal Ecosystem Research and Monitoring Sites (BERMS) program (<http://berms.ccrp.ec.gc.ca>), and since 2002, as part of the Fluxnet-Canada Research Network (<http://www.fluxnet-canada.ca>). A primary goal of these programs is to characterize the biophysical and climatic controls on the carbon, water and energy balances of southern boreal forest. Three recent analyses of multiyear flux data from SOA have contributed to this goal. Griffis *et al.* (2004) identified two key responses of  $F_{NEP}$  to interannual climatic variability: decreased  $R$  resulting from drought and increased  $P$  resulting from a phenological response to warm springs. Barr *et al.* (2004) evaluated annual  $F_{NEP}$  in relation to the phenology of LAI and found that the climatic factors that control leaf phenology and annual maximum LAI, such as spring temperature and drought, have a greater impact on  $F_{NEP}$  than climatic factors that affect  $R$  and  $P$  directly, such as growing-season temperature and soil water. Kljun *et al.* (in press) evaluated the response to drought of the three BOREAS/BERMS mature forest stands, including SOA and two coniferous sites, and found the greatest response at SOA.

The objectives of this study are to elucidate the climatic and biophysical factors that control the carbon and water balances at SOA over both seasonal and

multiyear time scales, and to separate their effects on  $R$  and  $P$ . Special attention is given to the coupling of the carbon and water cycles. We develop a new approach to characterize the seasonal and interannual variations in  $R$  and  $P$  that enables a clear separation of the effects of canopy duration and drought on the carbon and water cycles. We also explore the potential response of southern deciduous boreal forests to future climate change.

## Materials and methods

### Site description

The SOA site ( $53.7^{\circ}\text{N}$ ,  $106.2^{\circ}\text{W}$ , altitude 601 m) is a mature deciduous broadleaf forest at the southern edge of the Canadian boreal forest in Prince Albert National Park, Saskatchewan, Canada. The forest canopy has two distinct layers: a 22 m trembling aspen overstory (*Populus tremuloides* Michx) with ~10% balsam poplar (*Populus balsamifera* L.) and a 2 m hazelnut understory (*Corylus cornuta* Marsh with sparse alder (*Alnus crispa* (Alt.) Pursch). The forest regenerated after a natural fire in 1919 and had a 1998 stand density of ~830 stems  $\text{ha}^{-1}$ . The soil is an Orthic Gray Luvisol with an 8–10 cm deep surface organic LFH layer overlying a loam to sandy clay loam mineral soil. 30% of the fine roots are in the LFH layer and 60% are in the upper 20 cm of mineral soil. The terrain is generally level. Mean annual air temperature and precipitation at the nearest long-term weather stations are  $0.5^{\circ}\text{C}$  and 406 mm respectively (Prince Albert Airport,  $53^{\circ}13'\text{N}$ ,  $105^{\circ}41'\text{W}$ , altitude 428 m, 1942–1990 climatic normals) and  $0.3^{\circ}\text{C}$  and 456 mm, respectively (Waskešiu Lake,  $53^{\circ}55'\text{N}$ ,  $106^{\circ}04'\text{W}$ , altitude 532 m, 1934–1990 climatic normals).

### Climatic and biophysical measurements

Air temperature ( $T_a$ ) was measured at 36 m above ground level using a Vaisala model HMP35cf or HMP45cf temperature/humidity sensor (Vaisala Oyj, Helsinki, Finland) in a 12-plate Gill radiation shield (R. M. Young model 41 002-2, Traverse City, MI, USA). Soil temperature ( $T_s$ ) was measured using thermocouples in two profiles at depths of 2, 5, 10, 20, 50 and 100 cm. The two upper measurements were in the forest-floor LFH. In 1994, soil volumetric water content ( $\theta$ ) was measured using two horizontally oriented, 30 cm-long time-domain-reflectometry (TDR) probes at 8 and 15 cm depths and a vertically oriented, 1.2 m-long segmented TDR probe (Moisture Point type B, Gabel Corp., Victoria, Canada) (Blanken *et al.*, 2001). In April 1996, we installed eight of the 1.2 m-long segmented TDR probes at 10 m intervals, with measurements at depths of 0–15, 15–30, 30–60, 60–90 and 90–120 cm.

Three of the eight probes, which were most free of data gaps, were used in this analysis. We also measured  $\theta$  at 2.5 and 7.5 cm depth in the forest-floor LFH layer using two profiles of soil moisture reflectometers (model CS615, Campbell Scientific Inc., Logan, UT, USA), inserted horizontally in April 1996. Both measurement systems were calibrated in the laboratory using soil samples from the site, with independent calibration for each soil horizon. Unless otherwise stated, the mean  $\theta$  value was calculated for the 0–30 cm layer, which contained 90% of the fine root mass (Jagtar Bhatti, Canadian Forest Service, personal communication). Water table depth was measured using a high-resolution, vibrating-wire pressure transducer (Geokon model 4580-2, Lebanon, NH, USA) in a piezometer tube located 1 km east of the flux tower.

The LAI was measured using the LAI 2000 plant canopy analyzer (LI-COR Inc.). The seasonal LAI cycle was reconstructed using a robust methodology based on associated radiation and temperature indices (Barr *et al.*, 2004). We will denote the LAI of the forest overstory (mostly trembling aspen) and understory (mostly hazelnut) as  $L_a$  and  $L_h$ , respectively, and the annual maximum LAI during the fully leafed period as  $L_x$ .

The up- and downwelling photon flux densities of photosynthetically active radiation (PAR) above the forest canopy were measured using paired quantum sensors (model LI190SA, LI-COR Inc.). The downward-facing instrument was mounted on a boom, 4 m to the south of the tower and 10 m above the canopy. We estimated PAR absorption ( $Q_a$ ) by the canopy foliage based on Chen *et al.* (1999) but modified using Eqn (9) from Kucharik *et al.* (1998), as

$$Q_a = (Q_{\downarrow} - Q_{\uparrow}) \times \left[ \underbrace{1e^{-k_a \Omega_{ae} L_a}}_{\text{aspen}} + \underbrace{e^{-k_a (\Omega_{ae}(L_a+S)+\delta B_{ae})} (1e^{-k_h \Omega_h L_h})}_{\text{hazelnut}} \right], \quad (1)$$

where  $Q_{\downarrow}$  and  $Q_{\uparrow}$  are the down- and upwelling PAR photon flux densities above the canopy,  $k_a$  and  $k_h$  are PAR extinction coefficients for the aspen and hazelnut canopies (0.540 and 0.756, respectively, Blanken *et al.*, 1997),  $\Omega_{ae}$  is the aspen leaf clumping index at a zenith angle of  $35^{\circ}$  (0.69),  $S$  is the (hemisurface) aspen stem area index (0.40),  $B_{ae}$  is the effective (hemisurface) aspen branch area index (0.44),  $\delta$  is the fraction of  $B_{ae}$  that is exposed to gaps in the canopy (see Kucharik *et al.*, 1998) and  $\Omega_h$  is the hazelnut leaf clumping index (0.98). Annual  $Q_a$  was computed by integrating Eqn (1) over 1 year, using daily estimates for  $L_a$  and  $L_h$  (Barr *et al.*, 2004). The light-use efficiency for photosynthesis ( $\varepsilon$ ) was estimated as

$$\varepsilon = P/Q_a. \quad (2)$$

### Carbon, water and heat fluxes

Eddy-covariance measurements of the carbon dioxide, latent heat ( $\lambda E$ ) and sensible heat ( $H$ ) flux densities were made at 39 m from above a twin scaffold tower, 18 m above the forest canopy. The surface fluxes were calculated as the sum of the eddy flux at 39 m and the rate of change of storage in the air layer below 39 m. Continuous flux measurements were made from February to September 1994 and beginning in March 1996. The flux system consisted of a tri-axial sonic anemometer (model R2 or R3, Gill Instruments Ltd, Lymington, UK) in combination with a closed-path, thermostated, infrared gas analyzer (model LI6262, LI-COR Inc.), operated in absolute mode at the top of the tower. Additional details are given in Black *et al.* (1996) and Chen *et al.* (1999).

The surface CO<sub>2</sub> flux or net ecosystem exchange ( $F_{\text{NEE}}$ ) measures the net exchange of CO<sub>2</sub> between the ecosystem and the atmosphere. If we neglect the loss of carbon via groundwater flow, which is negligible at this site,  $F_{\text{NEE}}$  provides a direct measure of the net ecosystem productivity (i.e.  $F_{\text{NEP}} = -F_{\text{NEE}}$ ). Note that  $F_{\text{NEP}}$ , which results from the difference  $P - R$ , is positive for carbon sinks and that our sign convention gives positive signs to both  $R$  and  $P$ .

The procedure to fill gaps in  $F_{\text{NEP}}$  and to estimate  $R$  and  $P$  is described in Barr *et al.* (2004). Briefly, night-time  $F_{\text{NEP}}$  data were rejected when the friction velocity was below 0.35 m s<sup>-1</sup>. An energy-closure adjustment of +15% was applied to  $E$  and  $F_{\text{NEP}}$ .  $R$  was estimated as  $-F_{\text{NEP}}$  during periods when  $P$  was known to be zero, i.e. at night and during the cold season. Gaps in  $R$  were filled using an empirical ( $R = f(T_s)$ ) model, fit to the measured data. The model was used to fill gaps in  $R$  at night and to estimate  $R$  during the day.  $P$  was then estimated as  $F_{\text{NEP}} + R$  (daytime, warm-season periods) or zero (night-time and cold-season periods). Gaps in  $P$  were filled using an empirical light response curve, fit to the measured data. Although the methodology used to fill gaps in  $F_{\text{NEP}}$  and partition  $F_{\text{NEP}}$  between  $R$  and  $P$  introduced a small degree of uncertainty in the absolute magnitudes of  $R$  and  $P$ , sensitivity testing showed that the effects on annual  $F_{\text{NEP}}$  and the  $R/P$  ratio were relatively small.

We characterized seasonal and interannual changes in evapotranspiration using the evaporative fraction  $f_E$

$$f_E = \lambda E / (H + \lambda E). \quad (3)$$

The use of  $(H + \lambda E)$  in the denominator circumvented the issue of energy-balance closure.

Two canopy-scale, photosynthesis parameters were estimated from  $F_{\text{NEP}}$ :  $P_x$ , the light-saturated asymptote for  $P$ , and  $\phi$ , the ecosystem quantum yield. These

parameters were estimated by least-squares, nonlinear regression, based on the rectangular hyperbolic model (Hollinger *et al.*, 1999; Lee *et al.*, 1999; Saigusa *et al.*, 2002; Griffis *et al.*, 2003)

$$F_{\text{NEP}} = \phi P_x Q_\downarrow / (\phi Q_\downarrow + P_x) - R_d, \quad (4)$$

where  $R_d$  is the daytime, dark respiration. We evaluated the seasonal variations in  $P_x$ ,  $\phi$  and  $R_d$  by fitting Eqn (4) to measured, daytime  $F_{\text{NEP}}$  and  $Q_\downarrow$  data using a flexible, moving window of 240 measured (not-missing) data points, moved in increments of 48 points. The width of the moving window was typically 7–14 days but increased during periods with significant data gaps.  $R_d$  agreed closely with 5-day mean  $R$  (from above) but was not used in this analysis. Adding a temperature term to Eqn (4) did not improve the model performance.

We also fit an empirical model to the measured, night-time and cold-season  $R$  (i.e.  $-F_{\text{NEP}}$ ) data:

$$R = f_R \left[ \frac{a_1}{1 + e^{a_2(a_3 - T_s)}} \right], \quad (5)$$

where  $T_s$  is the soil temperature at 2 cm depth in the forest-floor organic layer,  $a_1$  to  $a_3$  are empirical constants and  $f_R$  is a time-varying parameter that quantifies the fractional departure of  $R$  from the mean 'wet'  $R$  vs.  $T_s$  relationship (the term inside the square brackets in Eqn (5), fit to high soil water data only). The value for  $f_R$  in Eqn (5) is independent of  $T_s$  at 2 cm and thus quantifies the effect of other time-varying factors on  $R$ , including (potentially)  $T_a$ ,  $T_s$  at other depths,  $\theta$ , LAI, root and shoot growth, soil microbial dynamics and the size of the labile carbon pool. The product  $f_R a_1$  gives the maximum  $R$  asymptote,  $a_2$  is a shape parameter and  $a_3$  is the soil temperature at which  $R$  reaches half of its asymptotic maximum. We fit the parameters in two steps. First, the constants  $a_1$  to  $a_3$  were fit to all measured (night-time)  $R$  and  $T_s$  data from periods with high soil water ( $\theta > 0.30$ ), with  $f_R$  fixed at 1.0. Second, the temporal variation in parameter  $f_R$  was fit using a flexible, moving window of 100 measured (not-missing) data points, corresponding to a period of 3–14 days. The window was moved in increments of 20 points. For each window,  $f_R$  was evaluated by linear regression, forced through the origin, of measured  $R$  vs. the term in the square brackets of Eqn (5). We used a narrower moving window for Eqn (5) than Eqn (4) because the exclusion of low- $u_*$  data at night produced a lower density of  $R$  data than  $P$  data. The use of Eqn (5) has two advantages over other empirical  $R$  models, such as annual exponential relationships: it is responsive to short-term and seasonal variations in  $R$  that are not driven by temperature and it gives conservative esti-

**Table 1** Interannual variability in annual total precipitation  $p$ , evapotranspiration  $E$ , net ecosystem production  $F_{\text{NEP}}$ , ecosystem respiration  $R$ , gross ecosystem photosynthesis  $P$ , PAR absorbed by the canopy foliage  $Q_a$ , the fraction of annual downwelling PAR absorbed by the canopy foliage  $Q_a/Q_{\downarrow}$  and the photosynthetic light-use efficiency  $\varepsilon$

Year	$p$ (mm yr <sup>-1</sup> )	$E$ (mm yr <sup>-1</sup> )	$F_{\text{NEP}}$ (g C m <sup>-2</sup> yr <sup>-1</sup> )	$R$ (g C m <sup>-2</sup> yr <sup>-1</sup> )	$P$ (g C m <sup>-2</sup> yr <sup>-1</sup> )	$Q_a$ (mol photons m <sup>-2</sup> yr <sup>-1</sup> )	$Q_a/Q_{\downarrow}$	$\varepsilon$ (mol C mol <sup>-1</sup> photons)
1994	466	447	206	1117	1323	3801	0.452	0.0290
1996	494	418	55	1162	1216	3215	0.381	0.0315
1997	413	517	131	1198	1330	3832	0.448	0.0289
1998	547	463	261	1137	1398	4392	0.505	0.0265
1999	479	413	119	1150	1269	3717	0.453	0.0284
2000	484	420	158	1099	1257	3590	0.433	0.0292
2001	235	445	367	1046	1413	4562	0.507	0.0258
2002	285	326	144	888	1032	3358	0.382	0.0256
2003	261	313	104	953	1057	3859	0.447	0.0228
1994–2003 (mean ± SD)	422 ± 103	418 ± 64	172 ± 94	1083 ± 103	1255 ± 135	3814 ± 436	0.445 ± 0.045	0.0275 ± 0.0026

The values for  $F_{\text{NEP}}$ ,  $R$  and  $P$  are slightly different from Barr *et al.* (2004) because of an additional postprocessing of the data. PAR, photosynthetically active radiation; NEP, net ecosystem production.

mates of  $R$  at high temperatures that may lie outside the range over which the model is fit.

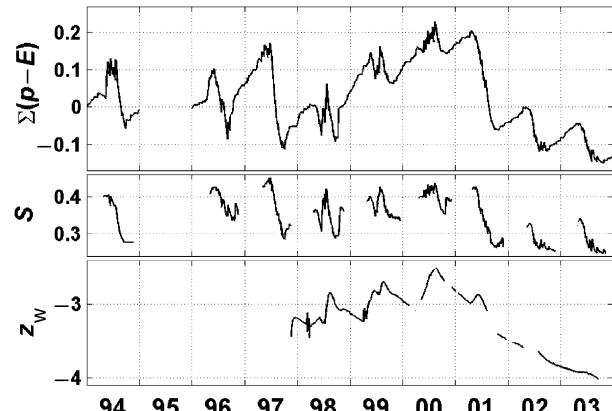
We used least squares, multiple linear regression to evaluate the dependence of  $P_x$ ,  $\phi$  and  $f_R$  on LAI,  $\theta$  and the day of year, and to evaluate the dependence of annual  $E$ ,  $R$  and  $P$  on several independent climatic and biophysical variables. For each dependent variable, regressions were run for all possible combinations of the independent variables, and the best-fit model was selected as the one that produced the lowest  $\alpha$  value (the probability of a type-one error). We also report the coefficient of determination ( $r^2$ ).

## Results and discussion

### Seasonal climate, water and carbon cycles

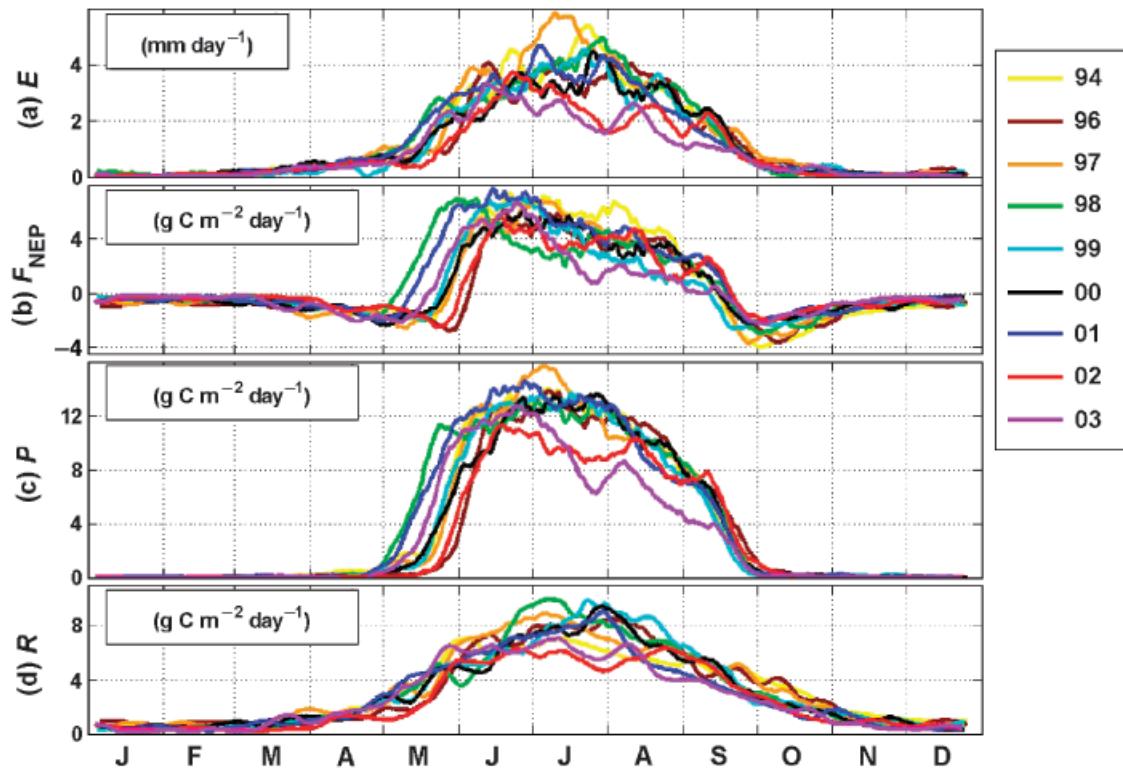
The 1994–2003 study period had two extreme climatic features: years with contrasting warm (1998 and 2001) and cool (1996 and 2002) springs, and a prolonged drought that began in July 2001 and extended throughout 2003 (Tables 1 and 2, Fig. 1). The interannual climatic differences caused large differences in canopy duration, related to the effect of spring temperature on the timing of leaf emergence (Barr *et al.*, 2004), and in drought stress, related to available soil water. Compared with the precipitation normals for 1900–2003 at the Prince Albert Airport, 1994 and 1996–2000 were average years whereas 2001–2003 were dry, each below the 10th percentile. The 2001–2003, 3-year precipitation total of 782 mm was the lowest on record, 159 mm below the previous minimum.

Figure 1 shows the vertical water balance at SOA for 1994–2003. We believe that there was little lateral water



**Fig. 1** Long-term vertical water balance at the BERMS Old Aspen site, including cumulative precipitation  $p$  minus evapotranspiration  $E$ , soil water storage  $S$  in the top 1.2 m of soil, and water table depth  $z_w$ . All terms have units of m. Soil water storage is shown during periods when the soil is not frozen.

loss from this site, so that cumulative precipitation minus evapotranspiration ( $p-E$ ) quantifies the net gain or loss of water at the site. Cumulative  $p-E$  shows a strong seasonal cycle, with net water gains during winter snow accumulation balanced by net water losses during most growing seasons when  $E$  exceeded  $p$ . At a multiyear time scale, there was a net water recharge of ~300 mm during the relatively wet years of 1997–2000 and a net water drawdown of ~350 mm during the drought years of 2001–2003. Cumulative  $p-E$  was coupled to changes in soil water and water table depth at both seasonal and multiyear time scales, as found by Blanken *et al.* (2001) for 1994 at SOA. Soil-water storage in the upper 1.2 m varied by ~150 mm in most years, with periods of drawdown by evapotranspiration



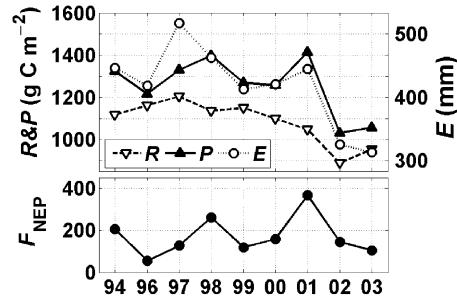
**Fig. 2** Annual cycles of 10-day running-mean evapotranspiration  $E$ , net ecosystem production  $F_{\text{NEP}}$ , gross ecosystem photosynthesis  $P$  and ecosystem respiration  $R$ .

balanced by periods of recharge from snowmelt and rainfall. The 2001–2003 drought completely depleted available soil water in the upper 1.2 m; the 200 mm of soil-water drawdown for that layer during 2001–2003 matches an independent estimate of 190 mm for available soil water, based on field capacity and wilting point. The total depletion of available soil water highlights the severity of the drought. The corresponding net water loss ( $P-E$ ) of 350 mm for 2001–2003 included extraction of 150 mm from depths below 1.2 m, associated with a 1.0 m drop in the water table.

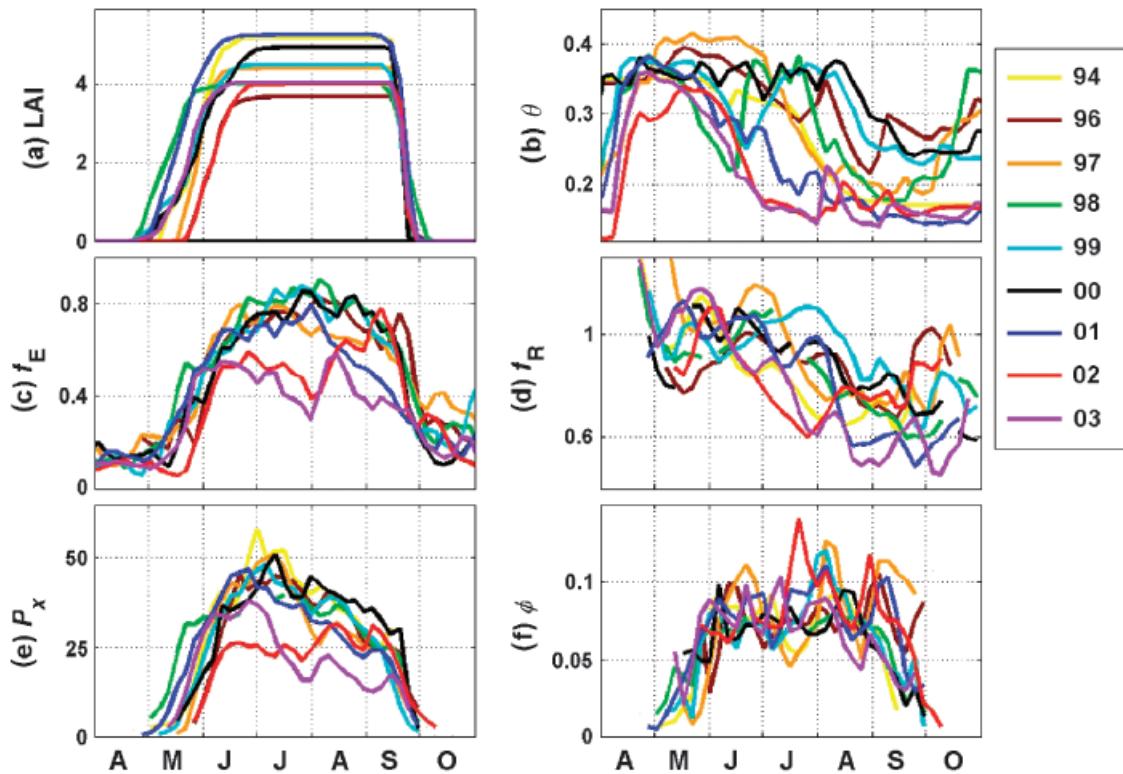
Figure 2 shows interannual variability in the seasonal cycles of 10-day mean  $E$ . The seasonal  $E$  cycle had three characteristic phases: a rapid rise during leaf emergence in May and early June, a broad seasonal plateau with a subtle decline during late June and July, and a gradual decline in August and September. The primary interannual differences occurred in summer and were related to differences in available soil water. Interannual differences in the timing of leaf emergence in spring affected  $E$  but the impact was less distinct for  $E$  than for  $F_{\text{NEP}}$  or  $P$ .

Figure 2 also shows interannual variability in the annual cycles of 10-day mean  $F_{\text{NEP}}$ ,  $R$  and  $P$ . Table 1 and Fig. 3 give annual totals.  $F_{\text{NEP}}$  rose sharply during leaf emergence in spring, declined slowly during the fully leafed period and dropped sharply during leaf

senescence in autumn. The seasonal minima in  $F_{\text{NEP}}$  occurred before leaf out and after leaf fall, with small but persistent negative values throughout the cold season. Interannual variability in the annual  $F_{\text{NEP}}$  cycle was highest during leaf emergence in spring, intermediate during the fully leafed and leaf-senescence periods, and lowest during the leaf-less period. Interannual differences in  $F_{\text{NEP}}$  were driven primarily by difference in LAI, via the effect of LAI on  $P$  (Barr *et al.*, 2004; see 'Relating annual  $E$ ,  $R$  and  $P$  to simple climatic and biophysical variables' below).  $R$  was less variable among years than  $F_{\text{NEP}}$  and  $P$ . The annual  $R$  cycle



**Fig. 3** Interannual variability in annual evapotranspiration  $E$ , ecosystem respiration  $R$ , gross ecosystem photosynthesis  $P$  and net ecosystem production  $F_{\text{NEP}}$ .



**Fig. 4** Annual cycles of 5-day running-mean (a) leaf area index LAI, (b) mean soil volumetric water content  $\theta$  (0–0.3 m), (c) evaporative fraction  $f_E$  (Eqn (3)), (d)  $f_R$  (Eqn (5)), (e)  $P_x$  ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ , Eqn (4)), and (f)  $\phi$  ( $\text{mol C mol}^{-1} \text{photons}$ , Eqn (4)).

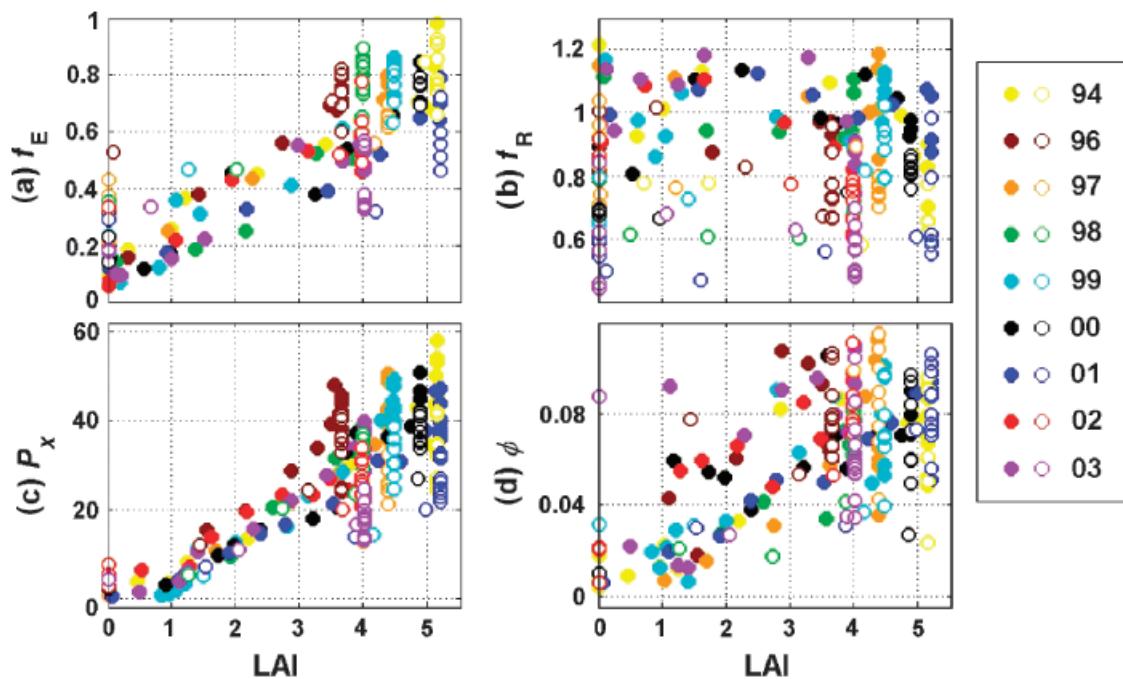
matched the seasonal rise and fall of  $T_s$  except that  $R$  peaked a little earlier than  $T_s$ . We attribute the subtle asymmetry in the annual  $R$  cycle to the seasonal drawdown in soil water and to asymmetry in the annual cycles of  $P$  and tree growth, both of which peak in late spring (Hogg *et al.*, 2005). Although  $R_h$  is closely coupled to temperature,  $R_a$  may be more dependent on  $P$  and tree growth (Janssens *et al.*, 2001).

#### Seasonal and interannual variations in biophysical parameters

**Evapotranspiration.** We characterized the annual  $E$ ,  $F_{\text{NEP}}$ ,  $R$  and  $P$  cycles based on empirical parameters from Eqns (3)–(5) (Fig. 4). The evaporative fraction  $f_E$  was controlled primarily by the seasonal phenology of LAI (Figs 4a, c and 5a) and secondarily by soil water (Figs 4b, c and 6a). During the leaf-less periods of early spring and autumn,  $f_E$  had a characteristic value of  $\sim 0.1$ – $0.2$ .  $f_E$  rose sharply during leaf emergence and dropped sharply during leaf senescence, with a broad, intervening plateau of  $\sim 0.7$ – $0.8$  during the fully leafed periods of nondrought years. Drought suppressed  $f_E$  during May–June 1998 and throughout August 2001–September 2003.

**Photosynthesis.** The photosynthetic parameters  $P_x$  and  $\phi$  (Eqn (4)) were tightly coupled to the seasonal LAI cycle (Figs 4e, f and 5c, d). The seasonal  $P_x$  cycles in Fig. 4e correspond to the idealized annual cycle of Wilson *et al.* (2001), including a linear increase during leaf emergence, a postleaf-emergence plateau, a gradual decline during the fully leafed period and a rapid decline during leaf senescence. The spring rise in  $P_x$  lagged leaf emergence by approximately 1 week;  $P_x$  began to increase at LAI of  $\sim 1.0$  and continued to increase until after the canopy was fully leafed. The lag in  $P_x$  vis-à-vis LAI during leaf emergence has been related to the continued increase in photosynthetic capacity beyond foliation, as the expanded leaves thicken and their Rubisco content increases (Normeets *et al.*, 2001).  $P_x$  was positively correlated with LAI and  $\theta$  ( $P_x [\mu\text{mol m}^{-2} \text{s}^{-1}] = -18.6 + 8.5 \text{ LAI} + 55 \theta$ ,  $r^2 = 0.75$ ,  $\alpha = 0.000$ ). In contrast to  $P_x$ ,  $\phi$  did not lag LAI during leaf emergence.  $\phi$  increased with LAI throughout leaf emergence, reached its annual maximum before full foliation and remained relatively constant during the fully leafed period, before its rapid drop during leaf senescence.

The summer decline in  $P_x$  is typical of temperate and boreal deciduous forests (Wilson *et al.*, 2000b, 2001). Previous studies have linked the  $P_x$  decline to the onset



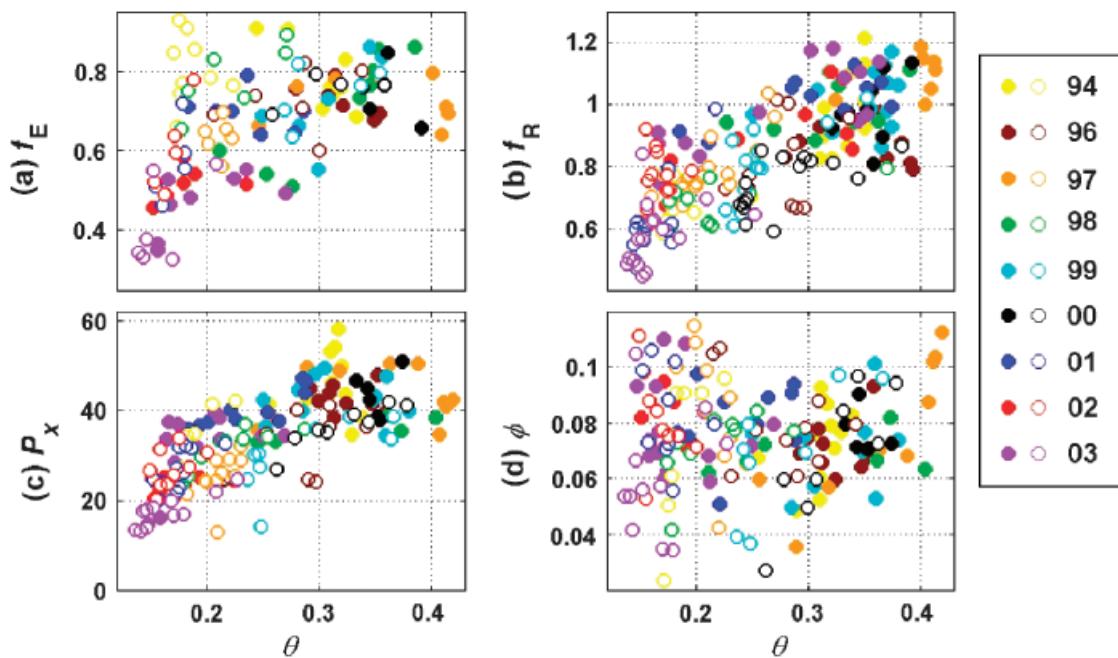
**Fig. 5** The relationship between empirical parameters from Eqns (3)–(5) and leaf area index LAI for periods when the soil was not frozen. The closed and open markers denote April–July and August–October, respectively.

of heat and drought stress (Wilson *et al.*, 2000b) and to leaf aging (Wilson *et al.*, 2000a, b; Normeets *et al.*, 2001). Our data support this conclusion. During the fully leafed period ( $LAI > 0.9 L_x$ ),  $P_x$  was positively correlated with soil water and negatively correlated with the day of year (DOY, used as an indicator of leaf age). The multiple linear regression relationship was  $P_x [\mu\text{mol m}^{-2} \text{s}^{-1}] = 36 + 78\theta - 0.10 \text{ DOY}$  ( $r^2 = 0.62$ ). Although both soil-water drawdown and leaf aging contributed to the growing-season decline in  $P_x$ , the primary influence was soil water. The growing-season decline in daily  $P$  (Fig. 2) thus resulted not only from shortening day length but also from leaf aging and the seasonal drawdown of soil water (Wilson *et al.*, 2001). The seasonal  $P_x$  cycle of deciduous forests is clearly dynamic and must be adequately characterized in process-based, ecosystem carbon-budget models, not only during leafout and senescence (Bondeau *et al.*, 1999; Botta *et al.*, 2000) but also during the fully leafed period (Wilson *et al.*, 2001).

**Respiration.** The primary factor controlling  $R$  was  $T_s$  at 2 cm depth, which accounted for 69% of the variation in  $R$  (Eqn (5), with the value of  $f_R$  fixed at 1.0). The influences of other environmental factors on  $R$ , such as, e.g.  $\theta$  and LAI, were captured in the temporal variation of parameter  $f_R$  (Eqn (5), Fig. 4d).  $f_R$  accounted for an additional 5.6% of the variation in  $R$ . This increase is similar to the increase in  $r^2$  from 0.69 to

0.74 that was achieved by adding  $\theta$  as a linear multiplier to Eqn (5), with  $f_R$  fixed at 1.0. The dependencies of  $f_R$  on LAI and  $\theta$  are shown in Figs 5b and 6b, respectively.  $f_R$  was highly correlated with  $\theta$  ( $f_R = 0.36 + 1.80\theta$ ,  $r^2 = 0.60$ ) but independent of LAI. Figures 6a–c show a subtle but significant difference in the responses of  $f_E$ ,  $f_R$  and  $P_x$  to  $\theta$ : all increased with  $\theta$  but  $P_x$  and  $f_E$  peaked at  $\theta \cong 0.30$  whereas  $f_R$  continued to rise. The implications are discussed in ‘Drought-induced reductions in annual  $R$  and  $P$ ’ below.

Our observation that  $R$  was independent of LAI differs from two recent studies. Griffis *et al.* (2004) analyzed the residuals from a temperature analysis of soil and bole respiration at SOA and found a weak coupling between respiration and  $P$ , suggesting a dependence of respiration on LAI. The dependence was stronger for bole than soil respiration. Gill *et al.* (1998) measured a peak in leaf respiration during leaf emergence in a mixed temperate deciduous forest, which they attributed to growth respiration. The difference between these results and Fig. 5b may be in the subtleness of the responses. Griffis *et al.*’s (2004) analysis shows that bole and leaf respiration accounted for 12% and 15%, respectively, of  $R$  at SOA, compared with 73% for soil respiration. Subtle changes in bole and leaf respiration with LAI or  $P_x$  are thus easily masked by the larger respiration from roots and soil. It is possible that the April–June vs. July–September contrast in  $f_R$  results in part from the decline in



**Fig. 6** The relationship between empirical parameters from Eqns (3)–(5) and mean soil volumetric water content  $\theta$  in the upper 0.3 m for periods when the canopy was fully leafed ( $LAI > 0.9L_x$ ). The closed and open markers denote April–July and August–October, respectively.

**Table 2** Regression coefficients ( $b_0$ ,  $b_1$  and  $b_2$ ), the coefficient of determination ( $r^2$ ) and the probability of a type-one error ( $\alpha$ ) for three multiple linear regression analyses, with annual  $E$ ,  $R$  and  $P$  as the dependent variables and the best-fit independent variables

Best-fit regression model	$b_0$	$b_1$	$b_2$	$r^2$	$\alpha$
$E (\text{mm yr}^{-1}) = b_0 + b_1 p_2$	208	0.25		0.54	0.024
$R (\text{g C m}^{-2} \text{yr}^{-1}) = b_0 + b_1 p_2 + b_2 T_a$	-147	0.62	47	0.91	0.001
$P (\text{g C m}^{-2} \text{yr}^{-1}) = b_0 + b_1 p_2 + b_2 \delta$	55	0.44	7.1	0.68	0.033

$p_2$ , 2-year precipitation total from the current and previous years;  $T_a$ , air temperature at 39 m;  $\delta$ , the canopy duration.

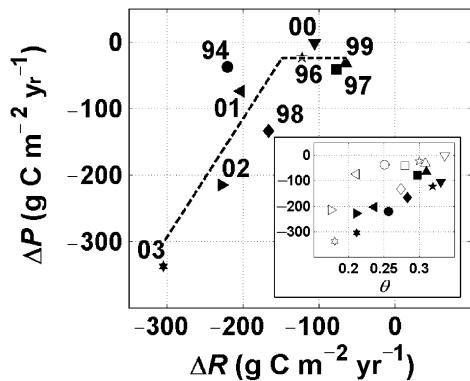
$P_x$  (Fig. 4d) and an associated decline in  $R_a$ , but we lack independent measurements of  $R_a$  to substantiate this.

#### Climatic and biophysical controls on annual $E$ , $R$ and $P$

**Relating annual  $E$ ,  $R$  and  $P$  to simple climatic and biophysical variables.** Figure 3 and Table 1 give annual total  $E$ ,  $R$ ,  $P$  and  $F_{\text{NEP}}$ .  $E$  varied among years by up to 207 mm (49% of the mean), with significant  $E$  depressions in 2002 and 2003 associated with the depletion of root-zone soil water (Fig. 1). Annual  $R$  and  $P$  were also lowest during the severe drought years of 2002 and 2003.  $P$  and  $E$  were tightly coupled at both 10-day (Fig. 2) and annual (Fig. 3) time scales, with very similar temporal patterns and anomalies. Although annual  $F_{\text{NEP}}$  was also low during 2002 and

2003, four of the nondrought years (1996, 1997, 1999 and 2000) had similarly low values.

In an earlier paper describing the seasonal phenology of LAI at SOA, Barr *et al.* (2004) reported a multiple linear regression analysis relating annual  $F_{\text{NEP}}$  to several climatic and biophysical variables. The best fit was found using two independent variables – the canopy duration and the annual maximum LAI. Annual  $F_{\text{NEP}}$  increased by  $6.9 \text{ g C m}^{-2}$  for each additional day in full leaf and  $83 \text{ g C m}^{-2}$  for each additional unit of LAI. Table 2 reports a similar analysis for annual  $E$ ,  $R$  and  $P$ . The analysis included nine independent variables: mean annual  $T_a$ , mean April–May  $T_a$ , mean growing-season  $T_a$ , mean growing season  $T_s$ , mean growing season  $\theta$ , total annual precipitation, total precipitation from the current and previous years,  $L_x$  and canopy duration



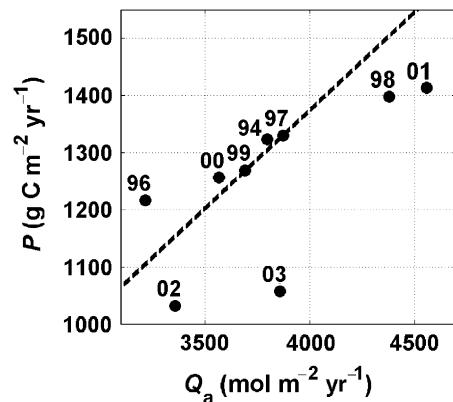
**Fig. 7** Annual, drought-induced changes in  $P$  and  $R$ , integrated over the full-leaved period for  $P$  and the period when the soil was not frozen for  $R$ . The dashed line was fit as two line segments, assuming that  $\Delta P$  leveled off at high values of  $\Delta R$ . The inset shows the variation of  $\Delta P$  (open symbols) and  $\Delta R$  (closed symbols) with mean soil volumetric water content  $\theta$  in the upper 0.3 m, averaged over the same periods as  $\Delta P$  and  $\Delta R$ .

(defined, following Norby *et al.* (2003) and Barr *et al.* (2004), as the number of days with  $LAI > 0.5L_x$ ). The best fit for  $E$  was found with only one independent variable – the total, two-year precipitation. The best fits for  $R$  and  $P$  used two independent variables: 2-year precipitation and mean growing-season  $T_a$  for  $R$ , and 2-year precipitation and canopy duration for  $P$ . The inclusion of 2-year precipitation in each of the best-fit models for  $E$ ,  $R$  and  $P$  highlights the impact of the 2001–2003 drought. In the corresponding  $F_{NEP}$  analysis (Barr *et al.*, 2004), 2-year precipitation did not contribute to the best-fit model because the drought suppressed both  $R$  and  $P$ . Indeed, in some drought years (e.g. 2001), the drought-induced reduction in  $R$  exceeded the reduction in  $P$ , producing an increase in  $F_{NEP}$  (Griffis *et al.*, 2004).

*Interannual variability in the R/P ratio.* The  $R/P$  ratio and the related ratio  $F_{NEP}/R$  are useful diagnostics in studies of interannual and intersite variability (Valentini *et al.*, 2000; Law *et al.*, 2002). At SOA, the annual  $R/P$  ratio ranged from 0.74 to 0.96 (mean 0.87, SD 0.06). The significance of  $R/P$  to interannual variability in  $F_{NEP}$  is shown by re-expressing  $F_{NEP}$  as the product of two terms:

$$F_{NEP} = (1 - R/P)P. \quad (6)$$

At SOA, decomposition of the variance of this product (Goodman, 1960) showed that interannual variability in  $F_{NEP}$  was dominated by the variance in  $(1 - R/P)$ . The two warm-spring, high- $F_{NEP}$  years had the lowest  $R/P$  ratios (0.74 in 2001 and 0.81 in 1998) whereas the coolest-spring, lowest- $F_{NEP}$  year (1996) had the highest  $R/P$  ratio (0.96). The  $R/P$  ratio during the other cool-



**Fig. 8** Annual gross ecosystem photosynthesis  $P$  as a function of photosynthetically active radiation absorbed by the canopy foliage  $Q_a$  (Eqn (1)). The dashed line shows the median photosynthetic light-use efficiency  $\varepsilon$  ( $0.0284 \text{ mol C mol}^{-1} \text{ photons}$ ).

spring year (0.86 in 2002) was intermediate because of the concurrent, moderate drought, which suppressed  $R$  more than  $P$ . The  $R/P$  ratio at SOA was slightly lower than the two proximate BERMS mature coniferous forest sites (Kljun *et al.*, in press): Southern Old Black Spruce (0.93) and Southern Old Jack Pine (0.95), and slightly higher than the European forest mean (0.80, Janssens *et al.*, 2001). Law *et al.* (2002) reported a range in  $R/P$  across a broad diversity of terrestrial ecosystems from 0.55 to 1.2, with means of 0.82 for deciduous broadleaf forest and 0.85 for coniferous forest. Many of the boreal and northern temperate forests had  $R/P$  ratios that exceeded 1.0. Valentini *et al.* (2000) found a strong dependence of  $R/P$  on latitude across a north–south transect of European forests, with values ranging from  $\sim 0.50$  for southern forests to  $\sim 0.90$  for northern forests. At  $54^\circ\text{N}$ , the latitude of the BERMS sites, their analysis gave  $R/P$  of  $\sim 0.85$ , in close agreement with SOA. The agreement is surprising because there are no European sites at  $54^\circ\text{N}$  with comparable climate and vegetation to SOA. We conclude that interannual variability in  $R/P$  at SOA was lower than global intersite variability but comparable to intersite variability among a diverse range of mature forest ecosystems in similar geographic and climatic regions.

Linear regression of annual  $R$  vs.  $P$  at SOA showed  $R = 0.55P + 399 \text{ g C m}^{-2} \text{ yr}^{-1}$  ( $r^2 = 0.52$ ,  $\alpha = 0.029$ ). These statistics were strongly influenced by the drought years of 2002 and 2003. The slope (0.55) is similar to the  $R_a/P$  ratio of  $0.53 \pm 0.04$  reported by Waring *et al.* (1998) for a range of temperate coniferous and deciduous forests. The similarity is intriguing and suggests that  $R_a/P$  is not only conservative among stands but also among years. The  $y$ -intercept of  $399 \text{ g C m}^{-2} \text{ yr}^{-1}$  would then represent the mean annual  $R_h$ . However, this hypo-

thesis is speculative because we lack independent measurements of net primary production (NPP),  $R_a$  or  $R_h$  to substantiate it. In addition, the precise values of the slope and  $y$ -intercept are uncertain; the 95% confidence intervals on the slope were  $\pm 0.48$ .

*Drought-induced reductions in annual R and P.* To quantify the responses of  $R$  and  $P$  to drought, we compared measured (30 min)  $R$  and  $P$  values with estimates  $R^*$  and  $P^*$  from empirical models that were fit to high soil water data only.  $P^*$  was estimated as the first term on the right side of Eqn (4) using fixed values of  $P_x$  ( $42 \mu\text{mol C m}^{-2} \text{s}^{-1}$ ) and  $\phi$  ( $0.059 \text{ mol C mol}^{-1} \text{ photons}$ ), which were in turn estimated from all measurements with  $\text{LAI} > 0.9L_x$  and  $\theta > 0.25$ .  $R^*$  was estimated from Eqn (5) (with  $f_R$  set to 1.0), with parameters  $a_1$  ( $11.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ),  $a_2$  (0.26) and  $a_3$  ( $9.5^\circ\text{C}$ ) estimated from all periods with  $\theta > 0.30$  and  $T_s > 0.0^\circ\text{C}$ . The different  $\theta$  thresholds for  $R$  and  $P$  were based on a visual inspection of the  $P_x$  vs.  $\theta$  and  $f_R$  vs.  $\theta$  relationships. We will denote the departures in  $R$  and  $P$ , relative to estimates from the high soil–water relationships, as  $\Delta R = R - R^*$  and  $\Delta P = P - P^*$ , respectively. To avoid the confounding influence of LAI on  $P$ ,  $\Delta P$  was estimated only when the canopy was fully leafed ( $\text{LAI} > 0.9L_x$ ).

The seasonal cycles of  $\Delta R$  and  $\Delta P$  varied significantly among years and were tightly coupled to differences in soil water. Figure 7 compares annual estimates of  $\Delta P$ , integrated over the fully leafed period, with annual estimates of  $\Delta R$ , integrated over the period when the soil was not frozen. The inset shows  $\Delta P$  and  $\Delta R$  as functions of  $\theta$  for the same periods.  $\Delta R$  increased with increasing  $\theta$ , with a difference between extreme dry and wet years of more than  $200 \text{ g C m}^{-2} \text{ yr}^{-1}$ . In contrast,  $\Delta P$  was relatively constant for mean annual  $\theta$  above 0.20 but dropped sharply as  $\theta$  fell below 0.20, with a net change of  $\sim 300 \text{ g C m}^{-2} \text{ yr}^{-1}$  between normal and extreme dry years.  $\Delta R$  was more sensitive than  $\Delta P$  to short dry spells that dried the soil LFH layer without significantly drawing down root-zone soil water, but much less sensitive than  $\Delta P$  to deeper, more extreme drought events. The ( $\Delta R$ ,  $\Delta P$ ) values fell into three groups: 1996, 1997, 1999 and 2000, moist (nondrought) years in which both  $\Delta P$  and  $\Delta R$  were small in magnitude; 1994, 1998 and 2001, moderate drought years in which both  $\Delta R$  and  $\Delta P$  increased in magnitude and  $\Delta R$  exceeded  $\Delta P$ ; and 2002 and 2003, severe drought years in which both  $\Delta P$  and  $\Delta R$  were large in magnitude. The drought effect on  $F_{\text{NEP}}$  thus varied with drought severity and history. Moderate drought enhanced  $F_{\text{NEP}}$  by suppressing  $R$  more than  $P$ . Severe and persistent drought suppressed  $F_{\text{NEP}}$  by suppressing  $P$  to a degree that matched or exceeded the large suppression in  $R$ . During the moderate drought years, drought events that

occurred early in the growing season (1998) suppressed both  $R$  and  $P$  whereas drought events that occurred late in the growing season (1994 and 2001) suppressed  $R$  more than  $P$ . The sensitivity of  $R$  and  $P$  to  $\theta$  highlights the need to include a realistic water cycle in ecosystem carbon models.

The contrasting responses of  $\Delta R$  and  $\Delta P$  to years of mild vs. severe drought may reflect different responses of  $R_a$  and  $R_h$  to soil drying. There are two related hypotheses that are consistent with Fig. 7, first that the  $R_a/P$  ratio is constant, not only among sites (Landsberg & Waring, 1997; Waring *et al.*, 1998), but also among years, and second, that soil microbes respond sensitively to the rapid drying of the forest floor whereas vegetation, which has access to deeper soil water, responds only to the drying of the entire root zone (Borken *et al.*, 1999, 2006). If both hypotheses are true, then the interannual differences in  $\Delta R$  during mild drought years at SOA, when  $\Delta P$  is small, would be caused by a suppression of  $R_h$  rather than  $R_a$ . This interpretation is supported by Borken *et al.* (2006), who used soil  $^{14}\text{CO}_2$  efflux in a temperate coniferous forest as an indicator of  $R_h$  and observed a sensitive response to experimentally imposed drought.  $R_a$  would be suppressed only during more severe drought years that also suppress  $P$ , with little further suppression of  $R_h$ . In Fig. 7, the slope of the  $\Delta R$  vs.  $\Delta P$  relationship during moderate-to-severe drought years (0.56, sloping dashed line) is similar to Waring *et al.*'s (1998) mature temperate forest  $R_a/P$  estimate of 0.53. It is also similar to the annual  $R$  vs.  $P$  slope at SOA (0.55, see 'Relating annual  $E$ ,  $R$  and  $P$  to simple climatic and biophysical variables' above). However, a recent study of a balsam fir forest, in which drought was imposed by excluding precipitation from control and root-exclusion plots, showed the opposite result; mild-to-moderate drought suppressed fine root growth and reduced  $R_a$  while having little impact on  $R_h$ , whereas more severe drought also suppressed  $R_h$  (Lavigne *et al.*, 2003, 2004). Measurements of seasonal fine-root dynamics that began in 2003 should help to clarify the responses of root vs. microbial respiration to drought. In addition, we are tracking the transient responses of  $R$  and  $P$  to the end of the drought, to see if a build-up of labile litter during the drought causes a transient, postdrought increase in  $R$  and decline in  $F_{\text{NEP}}$ .

*Interannual variability in P in relation to absorbed PAR.* Two previous studies of interannual variability at SOA (Black *et al.*, 2000; Barr *et al.*, 2004) concluded that the primary climatic control on  $F_{\text{NEP}}$  was spring temperature. Warm springs hasten leaf out, extend the canopy duration, increase PAR absorption and thereby increase  $P$  while having little effect on  $R$ . Figure 8 shows

annual  $P$  as a function of absorbed PAR (Eqn (1)). On an annual basis, the fraction of  $Q_{\downarrow}$  that was absorbed by the canopy foliage ranged from 38% in 1996% and 2002% to 51% in 1998 and 2001 (Table 1). The primary source of interannual variability in  $Q_a/Q_{\downarrow}$  was the timing of leaf emergence;  $L_x$  was important but secondary. Annual  $F_{\text{NEP}}$  and  $P$  were both positively correlated with  $Q_a$  ( $F_{\text{NEP}} = -541 \text{ g C m}^{-2} + 0.187 \text{ g C mol}^{-1}$  photons  $Q_a$ ,  $r^2 = 0.75$ ,  $\alpha = 0.003$ ;  $P = 463 \text{ g C m}^{-2} + 0.208 \text{ g C mol}^{-1}$  photons  $Q_a$ ,  $r^2 = 0.45$ ,  $\alpha = 0.049$ ) whereas annual  $R$  and  $Q_a$  were not correlated ( $\alpha = 0.82$ ). The  $1190 \text{ mol m}^{-2} \text{ yr}^{-1}$  (31%) increase in  $Q_a$  between the late and early leaf-emergence years was associated with a  $281 \text{ g C m}^{-2} \text{ yr}^{-1}$  increase in  $P$ .

The photosynthetic light-use efficiency ( $\varepsilon$ , Eqn (2)) varied among years by over 30%, from a minimum of  $0.0228 \text{ mol C mol}^{-1}$  photons during the extreme drought year of 2003 to a maximum of  $0.0315 \text{ mol C mol}^{-1}$  photons during the wet year of 1996. The  $\varepsilon$  median, characteristic of moist years with little drought stress, was  $0.0284 \text{ mol C mol}^{-1}$  photons. At hourly to weekly time scales,  $\varepsilon$  varied in relation to cloudiness, drought stress and the seasonal  $P_x$  cycle. However, when integrated over the growing season, the effect of cloudiness on  $\varepsilon$  was negligible. Mean growing-season  $\theta$  accounted for 60% of the variance in annual  $\varepsilon$ . Models that use  $\varepsilon$  to estimate seasonal and interannual variability in  $P$  and net primary productivity will need to incorporate the effects of drought (Turner *et al.*, 2003).

The corresponding  $\varepsilon$  for NPP at SOA was  $0.0142 \text{ mol C mol}^{-1}$  photons, based on Griffis *et al.*'s (2004) year-2000 estimate of 0.50 for the NPP/ $P$  ratio at this site. This NPP- $\varepsilon$  is ~40% higher than the typical value of 0.010 for boreal deciduous forests (Gower *et al.*, 1999; Anderson *et al.*, 2000), showing SOA to be a highly productive site, similar in many ways to temperate deciduous forests.

Figure 8 suggests a simple conceptual model for annual  $P$  with two primary controls. When water is not limiting, canopy duration and  $L_x$  control  $P$  via their influences on  $Q_a$ ;  $P$  varies in proportion to  $Q_a$  at constant, unstressed  $\varepsilon$  ( $0.0284 \text{ mol C mol}^{-1}$  photons at SOA). When water becomes limiting, water stress lowers  $\varepsilon$  independently of  $Q_a$  and causes  $P$  to decline to below the median  $\varepsilon$  line in Fig. 8. The reduction in  $\varepsilon$  is related to the associated reduction in  $P_x$  at low  $\theta$  (Fig. 6c). If we compare the impacts of the two controlling factors, we find interannual variations in  $P$  of ~30% associated with the variations in  $Q_a$  at constant  $\varepsilon$ , a 10% reduction in  $\varepsilon$  (and  $P$ ) during the drought years of 2001 and 2002, and a 20% reduction in  $\varepsilon$  (and  $P$ ) during the extreme drought year of 2003. We conclude that  $Q_a$  had the larger effect, despite the historic severity and duration of the 2001–2003 drought.

### Linkage to regional-scale and longer-term aspen responses

Many studies are showing the importance of climatic warming for northern deciduous ecosystems (Goulden *et al.*, 1996; Frolking, 1997; Myneni *et al.*, 1997; Black *et al.*, 2000; Baldocchi *et al.*, 2001). The potential impacts of a changing moisture regime are less certain. At SOA,  $F_{\text{NEP}}$  was relatively unaffected by the historic drought of 2001–2003 because the drought suppressed both  $R$  and  $P$ . This result reinforces the conclusion of Barr *et al.* (2004) that the primary impacts of climate change on boreal deciduous forests will be mediated through leaf phenology. There is a caveat. Observations of aspen dieback in the aspen parkland link tree mortality to the dual stresses of insect defoliation and drought and suggest a decline in forest productivity under a warmer and drier climate (Hogg *et al.*, 2002). Outbreaks of insects, notably the forest tent caterpillar (*Malacosoma disstria* Hbn.) can cause severe defoliation of aspen forests across large ( $>500 \text{ km} \times 300 \text{ km}$ ) areas (e.g. Hildahl & Reeks, 1960; Simpson & Coy, 1999), leading to dramatic growth reductions and potentially crown die-back (Hogg *et al.*, 2002; Frey *et al.*, 2004). At SOA, the forest was severely defoliated by insects in 1963–1964, 1979–1980 and 1992 (Hogg, 2001). Although the present study (1994–2003) was free of significant defoliation, we anticipate that, in the near future, the impact of insects will emerge as another major factor governing the interannual variation in carbon and water fluxes at this site.

Recently, Hogg *et al.* (2005) reported a regional scale, tree-ring analysis of pure aspen stands in 24 areas of the western Canadian interior, including the SOA site. At the regional scale, insect defoliation and moisture variation were the major factors governing interannual variation in aspen growth from 1951 to 2000. A subsequent resampling of tree rings in 2004 substantiated the importance of drought, showing a strong decrease in aspen growth during 2001–2003, both regionally and at SOA. The 2001–2003 drought was severe and affected large portions of western North America. Even at the healthy and productive SOA stand, the 2001–2003 drought caused a significant reduction in tree growth. The basal area increment at 1.3 m height, based on a sample of 18 trees, declined from  $0.56 \pm 0.08$  (1994–2001) to 0.39 and  $0.40 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1}$  (2002 and 2003, respectively). This reduction was coincident with a reduction in  $P$  from  $1315 \pm 73$  to  $1045 \pm 18 \text{ g C m}^{-2} \text{ yr}^{-1}$  for the same periods. The basal area increment  $\beta$  was positively correlated with  $P$  ( $\beta = -0.23 \text{ m}^2 \text{ ha}^{-1} \text{ yr}^{-1} + (0.061 \text{ m}^2 \text{ Mg}^{-1} \text{ C}) P$ ,  $r^2 = 0.67$ ,  $\alpha = 0.006$ ) but not significantly correlated with  $F_{\text{NEP}}$ . The pattern of past, interannual variation in growth based on tree rings at SOA (e.g. Hogg, 2001) was similar to that recorded for the region as a whole,

suggesting that the present results based on eddy covariance are generally applicable across much of the estimated 200 000 km<sup>2</sup> area of aspen-dominated forests in this region (Hogg *et al.*, 2002).

Given the strong linkage between carbon uptake by boreal deciduous forests and spring temperature that has been observed at this and other sites (Balodochi *et al.*, 2001), it is surprising that the regional scale, tree-ring analysis of Hogg *et al.* (2005) found that aspen tree growth (1951–2000) was more affected by interannual variation in moisture and insect defoliation than temperature. At the regional scale, cumulative growing degree days (1 April–31 July) were a significant but secondary factor. The estimated date of leaf emergence (based on cumulative growing degree days in spring) was not significantly correlated with tree growth. Hogg *et al.* (2005) gave two possible explanations of the regional-SOA anomaly: the absence of an insect-defoliation event at SOA during the eddy-covariance measurement period, which reduced the variance in basal area increment relative to the 1951–2000 mean, and the possibility that annual tree growth is more dependent on  $P$ , which is sensitive to drought, than  $F_{\text{NEP}}$  which is not. The anomaly may also be due to the inability of simple temperature indices to capture the actual interannual variability in canopy duration (White & Nemani, 2003).

At the landscape scale, future changes in the carbon and water budgets of the boreal forest are less certain. The boreal forest landscape is a highly disturbed and diverse mosaic, with stand-level carbon dynamics that are controlled by disturbance history, species composition, forest succession, soil drainage, water table depth and soil water retention. The response of  $F_{\text{NEP}}$  to future climate change will vary with ecosystem type, stand age and disturbance history, depending on the relative magnitudes of  $P$ ,  $R_a$  and  $R_h$  and the sensitivities of  $P$ ,  $R_a$  and  $R_h$  to changes in temperature and moisture. Phenological studies suggest that mature deciduous ecosystems will respond more positively than mature coniferous ecosystems to climatic warming because of the strong linkage between spring temperature and leaf emergence (Hunter & Lechowicz, 1992), with extended canopy durations enhancing  $P$  more than  $R$  (Black *et al.*, 2000; Barr *et al.*, 2004). Young forest stands may respond differently than mature stands to climate change because of differences in the relative magnitudes of  $R_a$  and  $R_h$ .

Whereas  $R_h$  is controlled primarily by soil temperature and moisture,  $R_a$  may be more influenced by the factors that affect  $P$  (Janssens *et al.*, 2001). However, we lack empirical data to confirm this. We also lack a simple and definitive method to separate  $R_a$  and  $R_h$ . The development of such a method will be pivotal to

further research progress. Other research priorities include improved understanding of the allocation and partitioning of carbon fluxes among above- and below-ground biomass, detritus and soil carbon pools, and improved understanding of the processes that govern the acclimation or persistence of the responses of  $P$ ,  $R_a$  and  $R_h$  to climate variability and change.

## Conclusions

Two extreme climatic features occurred in the 9-year study period (1994 and 1996–2003) that enabled analysis of climatic controls on the carbon and water cycles at seasonal and annual time scales: extreme warm and cool springs, which caused large interannual differences in canopy duration, and the severe 2001–2003 drought.

The seasonal LAI cycle controlled  $E$  and  $P$  but had little effect on  $R$ . The evaporative fraction ( $f_E$ ) and the light-saturated value for  $P$  ( $P_x$ ) had three characteristic phases: a rapid rise during leaf emergence in spring, a subtle decline during the fully leafed period, related to leaf aging and the drawdown of soil water, and a rapid decline during leaf senescence in autumn. Severe drought during the growing seasons of 2002 and 2003 suppressed  $f_E$  and  $P_x$  by as much as 50%.

Annual  $F_{\text{NEP}}$  varied among years from 55 to 367 g C m<sup>-2</sup> (mean 172, SD 94); the annual  $R/P$  ratio ranged from 0.74 to 0.96 (mean 0.87, SD 0.06). Interannual variability in  $F_{\text{NEP}}$  was controlled by factors that affected  $R$  and  $P$  differently.

Although drought suppressed both  $R$  and  $P$ , the net impact on  $F_{\text{NEP}}$  varied among years. Mild-to-moderate drought suppressed  $R$  while having little effect on  $P$ , causing  $F_{\text{NEP}}$  to increase. Severe drought suppressed both  $R$  and  $P$ , with a dramatic drop in  $P$  as drought intensified. The differential effects of drought on  $R$  and  $P$  suggested different responses of  $R_a$  and  $R_h$  to soil water stress, consistent with the hypothesis that the  $R_a/P$  ratio is constant.

The drought analysis provided new insight into the importance of canopy duration as the dominant climatic control of annual  $F_{\text{NEP}}$  in boreal deciduous forests. Interannual variability in  $P$  was controlled primarily by canopy duration and secondarily by drought, whereas interannual variability in  $R$  was controlled primarily by drought and secondarily by temperature. Because the drought effects on  $R$  and  $P$  partially offset each other, interannual variability in canopy duration (and  $P$ ) dominated  $F_{\text{NEP}}$ .  $P$  (mean 1255, SD 135 g C m<sup>-2</sup> yr<sup>-1</sup>) was more variable among years than  $R$  (mean 1084, SD 103 g C m<sup>-2</sup> yr<sup>-1</sup>).

The fraction of incoming PAR that was absorbed by the canopy foliage varied among years by over 30%,

driven by differences in the timing of leaf emergence. The photosynthetic light-use efficiency  $\varepsilon$  had a median value of  $0.0284 \text{ mol C mol}^{-1} \text{ photons}$  but was depressed by as much as 20% during severe drought years. The high value for  $\varepsilon$  showed SOA to be a highly productive boreal deciduous forest, with properties similar to many temperate deciduous forests.

This study reinforces the importance of studying the carbon and water cycles in consort. It also demonstrates the importance of long time series from flux-tower studies, many of which are just now becoming long enough to allow analysis of the complex, interacting climatic and biophysical controls on the carbon and water cycles of terrestrial ecosystems.

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