

# Impact of changing soil moisture distribution on net ecosystem productivity of a boreal aspen forest during and following drought

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## Abstract

The interannual and seasonal variability of gross ecosystem photosynthesis ( $P$ ), ecosystem respiration ( $R$ ) and evapotranspiration ( $E$ ), and their relationships to environmental factors were used to explain changes in net ecosystem productivity ( $F_{\text{NEP}}$ ) at the onset of, during, and following a 3-year-long (2001–2003) drought in a mature boreal aspen stand in central Saskatchewan, Canada. The forest was a moderate carbon (C) sink over its entire 11-year data record ( $F_{\text{NEP}} = 153 \pm 99 \text{ g C m}^{-2} \text{ year}^{-1}$ ), including the peak drought years of 2002 and 2003. In 2001, the depletion of water near the soil surface likely reduced heterotrophic soil respiration while water remaining deep in the root zone maintained  $P$  above the pre-drought mean, resulting in above-average  $F_{\text{NEP}}$ . In 2002 and 2003, the forest remained a C sink even though  $P$  was below average because  $R$  was also below average—a likely consequence of the influence of low soil water content in deep and shallow soil layers on both autotrophic and heterotrophic respiration. In 2004, the recharge of soil water in shallow soil layers allowed  $R$  to recover to its pre-drought values, whereas low spring temperatures, the slow recharge of soil water in deep soil layers in spring, late leaf emergence and diminished leaf area index combined to suppress  $P$  and produce the lowest annual  $F_{\text{NEP}}$  of the 11-year record ( $4 \text{ g C m}^{-2} \text{ year}^{-1}$ ). The low  $F_{\text{NEP}}$  and  $P$  were mirrored in the lowest stem growth and LAI values of the 11-year record. In 2005, a warm wet year, both the annual values and seasonal variations of  $F_{\text{NEP}}$ ,  $P$  and  $R$  returned to those of pre-drought years; the partial recovery of LAI to pre-drought values suggests that aspen  $P$  was able to adjust to this restriction on C assimilation. Growing season average dry surface conductance ( $g_{\text{sv}}$ ), the Priestley–Taylor coefficient ( $\alpha$ ) and light use efficiency (LUE) reached their lowest values in 2003 and became similar to pre-drought years in 2004–2005. Water use efficiency (WUE) was highest in 2003 and remained above average in 2004 and 2005. At the ecosystem scale, the above-average gains made in C sequestration in the first year of the drought were significantly offset by below-average stand  $F_{\text{NEP}}$  in the final 2 years of the drought, and in the year following the drought.

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## 1. Introduction

The terrestrial C budget of northern latitude ecosystems, and in particular that of the boreal forest, has

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received a great deal of attention because of their critical role in determining CO<sub>2</sub> concentration of the atmosphere and also due to their coupled influence on the Earth's climate. Concern about the likely impact of global climate and environmental changes has grown stronger within the scientific community in recent decades due to the predicted C cycle feedbacks in accelerating climate change (Pastor and Post, 1988; Rouse et al., 1997; Cox et al., 2000; Dufresne et al., 2002). Future climate perturbations are likely to result in substantial global and local changes to precipitation regimes (IPCC, 2001), which will alter exchange processes at the biosphere–atmosphere interface. Developing a clear understanding of the relationship between climate variability and ecosystem C exchange processes in the boreal forest is required to increase our confidence in modelling future C cycling–climate scenarios (Schaefer et al., 2002; Potter et al., 2003; Hashimoto et al., 2004).

Long-term coordinated experiments, satellite observations, and CO<sub>2</sub> modelling have revealed that the boreal forest in the northern hemisphere acts as a C sink (Keeling et al., 1996; Myneni et al., 1997; Sellers et al., 1997; Schimel et al., 2001). Boreal forests have also been found to act as a C source, with the annual C source/sink status of a particular stand depending on both the forest type and interannual variability in climate (Goulden et al., 1998; Schulze et al., 1999; Baldocchi et al., 2001; Gower et al., 2001; Law et al., 2002). There is concern that climate change could shift the C balance of the boreal forest from sink to source (Price and Black, 1990; Hollinger et al., 1998). This balance appears to be sensitive to growing-season length, growing-season climate, temperature and soil moisture as well as longer term trends in atmospheric CO<sub>2</sub> concentration and air temperature.

Increased summer continental drying and associated risk of drought at mid-latitudes have been cited as a likely consequence (66–90% chance) of global climate change in the 21st century (IPCC, 2001). Enhanced drought can result from decreases in annual precipitation, shifts in precipitation distribution over a region (Reichstein et al., 2002) and the timing of spring snowmelt (Barnett et al., 2005). Studies on the effects of severe, extended droughts on CO<sub>2</sub> exchange processes have been based either on short-term/seasonal observations, modelling (Law et al., 2001; Reichstein et al., 2002; Rambal et al., 2003; Ciais et al., 2005) or inferred from moderate drought effects (Goulden et al., 1996; Baldocchi, 1997; Goldstein et al., 2000; Barford et al., 2001; Anthoni et al., 2002). However, studies of ecosystem C balance response to severe moisture stress associated with long-term drought are still limited. The

recent 3-year-long drought of 2001–2003 over a large part of the western Canadian interior (Wheaton et al., 2005, <http://www.agr.gc.ca/pfra/drought/>), including the Southern Old Aspen (SOA) site in the Boreal Ecosystem Research and Monitoring Sites (BERMS) study area, presents an opportunity to improve our understanding of the response of CO<sub>2</sub> exchange processes as the ecosystem enters, passes through and emerges from a period of drought and this will be important in predicting the ecosystem's resilience to such possible climatic changes. During this period, extensive aspen dieback and mortality was noted in the more severely drought-affected areas across the region (Hogg et al., 2005), but was minimal at SOA.

Evapotranspiration rates of the deciduous stands in the southern boreal study area are relatively large compared to the wet evergreen sites that dominate the region (Baldocchi, 1997; Jarvis et al., 1997; Blanken et al., 2001). Thus, the greater water loss from the deciduous aspen stands in this area is thought to play an important role in regulating the local climate and promoting precipitation events during the growing season (Hogg et al., 2000) even though these stands represent only 15% of the land cover (Hall et al., 1997). The known vulnerability of aspen to warm climate has led to predictions of reduced growth and dieback of aspen forest owing to the drying climate over the southern boreal forest region (Hogg and Hurdle, 1995; Hogg et al., 2005). Earlier observations at SOA in the period 1994–2000 did not reveal any signs of severe moisture stress. However, SOA started showing signs of moisture stress by June 2001 (Griffis et al., 2004) and continued to show severe drought effects during 2002 and 2003. Kljun et al. (in press) found that the impact of the drought at SOA was greater than in an old black spruce stand and an old jackpine stand in the BERMS study area indicating the importance of topography, soil characteristics and the spatial distribution of precipitation in determining the effect of drought on local C sequestration. Barr et al. (in press) evaluated the climatic controls on C and water balances during 1994–2003 and identified canopy duration as the most important control on  $F_{NEP}$  at SOA. In this paper we focus on the recovery of the SOA ecosystem from the 3-year-long drought. The main objectives of the paper are to (1) examine the response of ecosystem CO<sub>2</sub> and water vapor exchange as the aspen stand entered, passed through and emerged from a 3-year drought, (2) elucidate the dynamics of ecosystem-scale photosynthesis and respiration responsible for the observed pattern in net ecosystem CO<sub>2</sub> exchange, (3) determine to what extent changes in ecosystem CO<sub>2</sub> exchange were

reflected in measurements of stand productivity, and (4) assess the relative importance of same-year environmental factors and residual drought effects, if any, in controlling the net ecosystem CO<sub>2</sub> exchange over the drought period and in the years following drought.

## 2. Materials and methods

### 2.1. Site

The study was conducted at SOA (53.7°N, 106.2°W, elevation 600 m), near the southern edge of boreal forest in Prince Albert National Park in central Saskatchewan, Canada. Based on the climate data from an Environment Canada Meteorological Station at nearby Waskesiu Lake (53.92°N, 106.07°W), the 1971–2000 mean annual temperature was 0.4 °C, and the mean annual precipitation was 467 mm. The soil, an Orthic Gray Luvisol, has a 8–10 cm deep surface organic layer with bulk density of about 160 kg m<sup>-3</sup> (Chen et al., 1999). The mineral soil has silty-clay texture and a bulk density of about 1300 kg m<sup>-3</sup>. Aspen roots were found at up to 120 cm depth with up to 26% of the total root length found below 60 cm depth (Van Rees, 1997). This site was regenerated after a natural fire event in 1919 resulting in an even-aged stand of trembling aspen (*Populus tremuloides* Michx.) with scattered balsam poplar (*Populus balsamifera* L.) and a mean canopy height of approximately 22 m, mean stem diameter at 1.3 m height of 20 cm (S.D. = 4.5 cm) and a stand density of 830 stems ha<sup>-1</sup>. The understory is dominated by hazelnut (*Corylus cornuta* Marsh.), about 2 m tall. The topography is generally level and the fetch is at least 3 km in all directions. The flux footprint at this site was found to spread along the prevailing wind direction up to 450–550 m during daytime convective conditions and 900 m during neutral or nighttime stable conditions (Kljun et al., in press). The study site was established in 1993 as part of the Boreal Ecosystem–Atmosphere Study (BOREAS) ([http://www-eosdis.ornl.gov/boreas/boreas\\_home\\_page.html](http://www-eosdis.ornl.gov/boreas/boreas_home_page.html)). Flux measurements were not made in 1995. After BOREAS, measurements at SOA have continued under the BERMS (<http://berms.ccrp.ec.gc.ca>) program and since 2002 as a part of the Fluxnet-Canada Research Network (<http://www.fluxnet-canada.ca>).

### 2.2. Measurement of fluxes of sensible heat, water vapor and CO<sub>2</sub>

Eddy covariance (EC) measurements of half-hourly turbulent fluxes of CO<sub>2</sub>, water vapor and sensible heat

were made at 39 m above the ground on a scaffold tower using a three-axis sonic anemometer (model R2 or R3, Gill Instruments Ltd., Lymington, Hampshire, UK) and a closed path infrared gas (CO<sub>2</sub>/H<sub>2</sub>O) analyzer (model LI-6262, LI-COR Inc., Lincoln, NE, USA) with a 4-m-long heated sampling tube. The former measured fluctuations in wind vector components and temperature, and the latter measured fluctuations in water vapor and CO<sub>2</sub> concentrations. The CO<sub>2</sub> concentration measurements were automatically calibrated once daily to correct for the zero and span shift using CO<sub>2</sub> standards from the Canadian Greenhouse Gases Measurement Laboratory (GGML) of the Meteorological Service of Canada in Downsview, ON, Canada. All GGML CO<sub>2</sub> measurements are directly traceable to the international absolute WMO mole fraction scale originally maintained by the WMO Central Calibration Laboratory at the Scripps Institute of Oceanography and from 1996 onwards by NOAA/CMDL. The analog signals from the EC instruments were sampled at 125 Hz with a data acquisition system (model DAQ-book 200, IOtech Inc., Cleveland, OH) and were digitally filtered and down sampled at 20.83 Hz to a computer for flux calculation. Half-hourly turbulent fluxes were calculated using the covariance of the fluctuations in vertical wind component and the scalar quantities, namely, air temperature for sensible heat, mole mixing ratio of water vapor for water vapor flux and mole mixing ratio of CO<sub>2</sub> for CO<sub>2</sub> flux (Webb et al., 1980). Further details on the experimental set up, calibration and calculation of turbulent fluxes can be found elsewhere (Chen et al., 1999; Griffis et al., 2003; Barr et al., 2004). The net exchange of CO<sub>2</sub> between the atmosphere and the ecosystem was determined as:

$$F_{\text{NEE}} = F_c + S_c \quad (1)$$

where  $F_{\text{NEE}}$  is the net ecosystem exchange,  $F_c$  the CO<sub>2</sub> flux density measured at the height of the EC sensors and  $S_c$  is the CO<sub>2</sub> storage flux (the rate of change of CO<sub>2</sub> storage in the air layer below the EC sensors per unit ground area) (Yang et al., 1999). Positive values of  $F_{\text{NEE}}$  mean loss of CO<sub>2</sub> by the ecosystem and gain by the atmosphere. In this study the measured fluxes were corrected for energy balance closure (88%) following Griffis et al. (2003).

### 2.3. Supplementary meteorological measurements

The measurement tower was also equipped with instruments to measure the upwelling and downwelling components of photosynthetically active radiation (PAR) (paired quantum sensors, model LI190SA, LI-COR Inc.),

shortwave radiation (paired pyranometers, model CM11, Kipp & Zonen, Delft, The Netherlands) and longwave radiation (paired pyrgeometers, model PIR The Eppley Laboratory Inc., Newport, RI, USA) and air temperature and humidity (model HMP-35C, Vaisala Oy., Helsinki, Finland). Precipitation was measured with a weighing rain gauge (Belfort Instruments, Baltimore, MD, USA) and an MSC tipping bucket rain gauge. Measurements of soil temperature (two profiles) at six depths between 2 and 100 cm were made with copper–constantan thermocouples. Volumetric soil water content was measured at 2.5 and 7.5 cm depth using soil water reflectometers (model CS 615, Campbell Scientific Inc., Logan, UT, USA) and TDR probes (Moisture Point type B, Gabel Corp., Victoria, Canada) at depths of 0–15, 15–30, 30–60, 60–90, and 90–120 cm. Leaf area index (LAI) was measured using a Plant Canopy Analyzer (model LAI-2000, LI-COR Inc.) (Barr et al., 2004). Temporal variation in aspen stem growth was determined by conducting tree-ring analysis as part of the Climate Change Impacts on the Productivity and Health of Aspen study in western Canada (Hogg et al., 2005). Stem growth values reported in this paper represent the estimated increment in stand basal area from the sampling of 18 stems (6 plots with 3 trees per plot) at the 1.3 m height in the fall of 2004. The sampling locations ranged from 200 to 5 km from the flux tower, and were all situated within the same extensive area dominated by 85-year-old trembling aspen trees. Methods of sampling and analysis followed those described in Hogg et al. (2005), except that 12 of the 18 stems were sampled using increment cores rather than by destructive sampling. Stem growth was updated to include 2005 through additional increment cores that were collected from 11 stems in the fall of 2005.

#### 2.4. Annual estimates of net ecosystem productivity, photosynthesis and respiration

Net ecosystem productivity ( $F_{\text{NEP}}$ ) was calculated as  $F_{\text{NEP}} = -F_{\text{NEE}}$ , which is a good approximation of C sequestration because the losses of dissolved organic C (DOC) are likely very small at this site.  $F_{\text{NEP}}$  is equal to the difference between gross ecosystem photosynthesis ( $P$ ) and ecosystem respiration ( $R$ ), i.e.,  $F_{\text{NEP}} = P - R$ , and is positive when  $P$  exceeds  $R$ .  $F_{\text{NEE}}$  is positive for C sources whereas  $F_{\text{NEP}}$  is positive for C sinks. Annual  $F_{\text{NEP}}$  was obtained by gap filling the missing half-hour flux data as well by replacing nighttime fluxes when turbulence was not fully developed (i.e. friction velocity ( $u_*$ ) was  $< 0.35 \text{ m s}^{-1}$ ) (Barr et al., 2002; Griffis et al., 2003). Up to 45% of the nighttime data were replaced as

a result of low  $u_*$  conditions. We followed the procedure described in Barr et al. (2004) to fill gaps in  $F_{\text{NEP}}$  and to estimate  $P$  and  $R$ . Briefly,  $R$  was estimated from nighttime and cold-season  $F_{\text{NEP}}$  data as  $R = -F_{\text{NEP}}$ , and an annual empirical relationship between  $R$  and soil temperature ( $T_s$ ) at a shallow depth was used to fill the gaps at night and estimate daytime  $R$ .  $P$  was estimated as  $F_{\text{NEP}} + \text{daytime } R$  or zero (night time and cold season) and the gaps in  $P$  are then filled using hyperbolic dependence of  $P$  on photosynthetically active radiation ( $Q$ ) (Michaelis–Menten light response equation). Gaps in  $F_{\text{NEP}}$  were then filled using modelled  $P-R$ . To account for changes in other environmental (e.g., soil moisture, atmospheric saturation deficit) or phenological (LAI) variables over a short period of time, a time varying factor, which was determined within a 100 point window as the slope of a linear regression of the modelled  $R$  (and  $P$ ) versus measured  $R$  (and  $P$ ) and was applied to each empirical relationship.

The uncertainties associated with the annual estimates of  $F_{\text{NEP}}$  were estimated as follows: (1) random error associated with the half-hourly fluxes was calculated by introducing a 20% error in half-hour  $F_{\text{NEP}}$  values following Morgenstern et al. (2004); (2) uncertainty due to the gap filling procedure was estimated using Monte Carlo simulation similar to Griffis et al. (2003) by generating gaps (up to 40% of the year) using a uniformly distributed random number generator, except that the continuous gaps were varied from a half hour to 10 days; (3) systematic error due to the selection of a  $u_*$  threshold was obtained by recalculating  $F_{\text{NEP}}$  while changing the  $u_*$  threshold by  $\pm 20\%$  of the value we used ( $0.35 \text{ m s}^{-1}$ ). Taking the square root of the sum of squares of the random error estimates ( $\pm 5$  and  $\pm 28 \text{ g C m}^{-2} \text{ year}^{-1}$  for (1) and (2), respectively) gave an overall random error for the annual estimates of  $F_{\text{NEP}}$  of  $\pm 29 \text{ g C m}^{-2} \text{ year}^{-1}$ . To obtain an estimate of the overall uncertainty, the systematic error was added to the random error directly (not in a sum-of-squares fashion) because the systematic error stemming from choosing a particular  $u_*$  value is not random and will be in the same direction with similar magnitude in all years. It was estimated to be  $\pm 21 \text{ g C m}^{-2} \text{ year}^{-1}$ , so that the maximum uncertainty of the annual estimates of  $F_{\text{NEP}}$  was  $\pm 50 \text{ g C m}^{-2} \text{ year}^{-1}$ .

#### 2.5. Canopy-level physiological response parameters

To better gauge the physiological response of the ecosystem to drought, several parameters indicating

canopy level water status were determined. The surface conductance  $g_{sv}$  to water vapor transfer was calculated by rearranging the Penman–Monteith equation (Monteith and Unsworth, 1990) to obtain:

$$\frac{1}{g_{sv}} = \left[ \left( \frac{s}{\gamma} \right) \beta - 1 \right] \left( \frac{1}{g_a} \right) + \frac{\rho c_p D}{\gamma \lambda E} \quad (2)$$

where  $s$  is the rate of change of saturation vapor pressure with temperature,  $\gamma$  the psychrometric constant,  $\beta$  the Bowen ratio ( $\beta = H/\lambda E$ ),  $g_a$  the aerodynamic conductance,  $\rho$  and  $c_p$  the density and specific heat of air, respectively,  $D$  the atmospheric saturation deficit,  $\lambda$  the latent heat of vaporization of water, and  $E$  is the water vapor flux (evapotranspiration).  $g_a$  was calculated using the equations given in Blanken et al. (1997). In open well-ventilated canopies such as the aspen stand in this study (Mahrt et al., 2000),  $g_{sv}$  calculated using Eq. (2) is largely determined by mean stomatal conductance and LAI (Kelliher et al., 1993). The daytime mean value of  $g_{sv}$  was calculated by averaging daytime  $g_{sv}$  values when downwelling PAR exceeded  $200 \mu\text{mol m}^{-2} \text{s}^{-1}$ . To ensure that wet leaf surfaces did not affect the estimates of  $g_{sv}$  (so that  $g_{sv}$  largely reflected the stomatal conductance of the canopy) data from all days when rain events occurred were excluded.

The Priestley–Taylor coefficient  $\alpha$  (Priestley and Taylor, 1972), which indicates the degree of soil water supply limitation of evapotranspiration, was estimated as

$$\alpha = \frac{\lambda E}{\lambda E_{eq}} = \frac{\lambda E}{[s/(s+\gamma)]R_a} = \frac{s+\gamma}{s(\beta+1)} \quad (4)$$

where  $E_{eq}$  is the equilibrium evaporation rate.  $R_a$  is the available energy flux, which is given by  $R_a = R_n - Q_j$ , where  $R_n$  is the net radiation flux and  $Q_j$  is the sum of all minor energy balance terms (i.e., soil heat flux, biomass heat storage rate, rate of sensible and latent heat storage in the air column beneath EC sensor height, and photosynthetic energy storage rate).  $\alpha$  was calculated using the last expression on the right hand side of Eq. (4) which was obtained by replacing  $R_a$  with  $H + \lambda E$  to avoid the issue of energy-balance non-closure (Barr et al., 2002). Generally, when  $\alpha \geq 1$ , there is a sufficient supply of soil water so that  $E$  is controlled by  $R_a$ . Daytime mean  $\alpha$  was calculated using daytime (downwelling  $Q > 200 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) means of  $s$ ,  $\gamma$  and  $\beta$ .

Water use efficiency ( $\text{WUE} = P/E$ ) is a measure of the amount of C taken up during photosynthesis relative to the water lost by the ecosystem ( $E$ ) and has been used to determine the adaptation and productivity of plants in water-limited areas (Xu and Hsiao, 2004). The mean

value of growing season WUE was estimated using growing season values of  $P$  and  $E$ . Most of growing season  $E$  was due to transpiration as Blanken and Black (2004) reported that the contribution from evaporation from the soil surface was  $<5\%$  and we estimated that the contribution of evaporation from wet leaves was  $<6\%$ . Light use efficiency is the ratio of mol of C biomass produced per mol quanta of PAR absorbed and was calculated as  $\text{LUE} = P/Q_a$ , where  $Q_a$  is the absorbed PAR (APAR) by the canopy foliage. APAR was estimated using Eq. (1) in Barr et al. (in press) with measured downwelling and upwelling PAR and daily estimates of aspen and hazelnut LAI (Barr et al., 2004). The fraction of the absorbed PAR (FPAR) was estimated as the ratio of PAR to APAR. In this paper, “growing season” refers to the number of days when  $24 \text{ h } F_{\text{NEP}} > 0$ , rather than days of detectable photosynthesis ( $P > 0$ ) used in Black et al. (2000) and Kljun et al. (in press) for SOA. The former definition was used because it resulted in less uncertainty and there was close agreement between it and “canopy duration” defined by Barr et al. (2004).

### 3. Results and discussion

#### 3.1. Interannual variation in climate and LAI

##### 3.1.1. Variation in climate and soil water content

Fig. 1 shows the interannual variation in the annual total downwelling PAR and precipitation, and annual and average spring (April–May) temperatures during 1994–2005. The lowest annual precipitation occurred

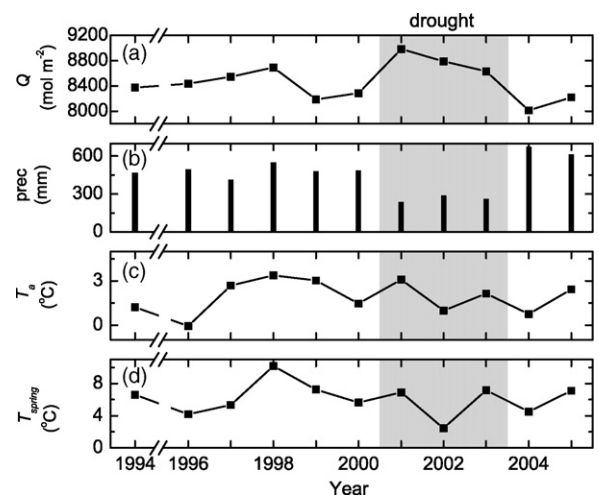


Fig. 1. Interannual variations in (a) annual total of downwelling photosynthetically active radiation, PAR ( $Q$ ), (b) precipitation (prec), (c) annual mean temperature ( $T_a$ ), and (d) spring (April and May) mean temperature ( $T_{\text{spring}}$ ) at SOA.

during the 3 drought years (2001–2003); the highest was measured in 2004. In all other years, the annual precipitation remained above or close to the 30-year mean value (467 mm). Not surprisingly, downwelling PAR was highest in 2001–2003. The lowest annual average temperatures were observed in 1996 and 2004. At this site, the spring temperature controls the timing of leaf emergence and hence the length of the growing season (Black et al., 2000; Barr et al., 2004). For the 2 years that followed the drought period, the spring of 2004 was the third coldest of the 11-year record while that of 2005 was similar to warm years. The cool weather of 2004 was associated with the lowest total annual downwelling PAR in the 11-year data record.

The effects of below-average precipitation in 2001–2003 on the average growing season volumetric soil water content ( $\theta$ ) in the shallow (0–0.15 m) and deep (0.6–0.9 m) soil layers are apparent from Fig. 2a and b. We considered moisture in both shallow and deep soil layers because an earlier study showed that up to 26% of the roots in aspen trees was found below 0.6 m (Van Rees, 1997). The small root densities found in the deeper layer likely play an important role in water and nutrient uptake. Values of  $\theta$  in the shallow layer began to decrease by June 2001 and continued to decrease through 2002 and 2003. The lowest value of average growing season  $\theta$  in this layer occurred in 2003 and was about 33% lower than the pre-drought mean value. Following the end of the drought, the average 2004 and

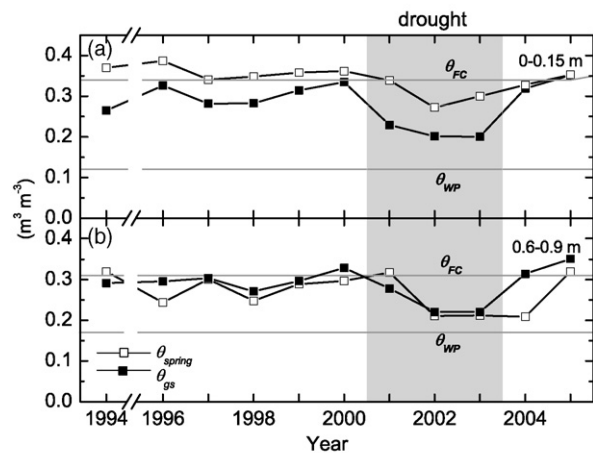


Fig. 2. Interannual variations in the spring (April–May) average and growing season average of soil water content ( $\theta$ ) in the (a) 0–0.15 m and (b) 0.60–0.90 m layers. The upper and lower solid lines in each panel represent soil  $\theta$  at field capacity,  $\theta_{FC}$  (–33 kPa soil water matric potential) and wilting point,  $\theta_{WP}$  (–1500 kPa soil water matric potential), respectively. The saturation water content for 0–0.15 and 0.6–0.9 m layers are  $\sim 0.45$  and  $\sim 0.37 \text{ m}^3 \text{ m}^{-3}$ , respectively.

2005 growing season  $\theta$  in both the shallow and deep layers recovered to near pre-drought values. However, while the average value of  $\theta$  for April and May ( $\theta_{\text{spring}}$ ) in the shallow layer (Fig. 2c) in 2004 was higher than those observed over the last 2 years of the drought, they remained slightly below the pre-drought mean value. Notably,  $\theta_{\text{spring}}$  in the deep layer (Fig. 2d) reached its lowest value of the 11-year record ( $0.209 \text{ m}^3 \text{ m}^{-3}$ ) in 2004, the year after the drought ended. The increased precipitation in 2004, recharged water in both shallow and deep soil layers and produced above-average  $\theta$  values for June 2004. In 2005, the recharged soils received annual precipitation above the 11-year mean, leading to  $\theta$  values well above the pre-drought mean through the spring and growing season. During the 3 drought years, the water table at this site dropped from 3 to 4 m depth (Barr et al., in press). The decline of  $\theta$  to values below the field capacity (FC;  $\theta_{FC} = \theta$  at –33 kPa soil water matric potential) and very close to the permanent wilting point (WP;  $\theta_{WP} = \theta$  at –1500 kPa soil water matric potential) in the peak drought years of 2002–2003 indicates the severity of the drought. Further evidence of the drought’s impact on soil moisture conditions can be seen in the changing relative available water content ( $\theta_{RA} = (\theta - \theta_{WP}) / (\theta_{FC} - \theta_{WP})$ ) in the 0–1.2 m soil profile, which dropped to minimum values of 0.50 in 2001, 0.40 in 2002 and 0.35 in 2003, which occurred near the end of the growing season.

### 3.1.2. Recovery of LAI following drought

The fully leafed values of LAI measured at this site from 1994 to 2005 are shown in Fig. 3. The high annual LAI in 2001 resulted from the favourable growing conditions during the previous years, with a steady increase in LAI from 1996 to 2001. During the peak years of the drought (2002–2003), aspen LAI dropped significantly, while hazelnut LAI dropped only slightly. There was a further reduction in both aspen and hazelnut LAI in the year following the drought (2004),

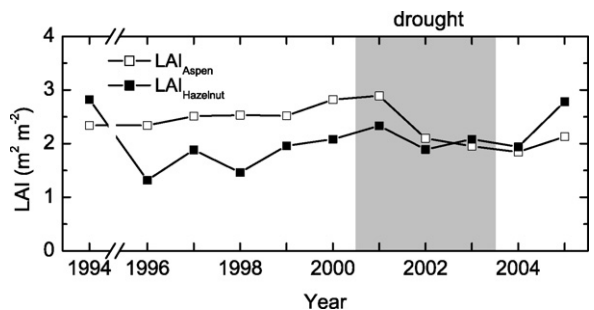


Fig. 3. Interannual variation in leaf area index (LAI) for the fully leafed canopy of aspen and hazelnut at SOA.

with the aspen LAI reaching its lowest value of the 11-year record. In 2005, hazelnut LAI rose sharply and aspen LAI rose slightly, showing the beginning of post-drought recovery. The recovery of the LAI of both species in 2005 resembled that following the 1992 defoliation of the aspen canopy by the outbreak of large aspen tortrix (*Choristoneura conflictana* [Walker]) when there was relatively fast recovery of hazelnut LAI together with a slow recovery of aspen LAI. Aspen LAI in 2005 was comparable to that in 1994, 2 years after the 1992 defoliation episode (Barr et al., 2004). The higher values of hazelnut LAI relative to aspen LAI in 2005 could have been the result of higher interception of PAR by the hazelnut understory due to the low aspen LAI. Aspen LAI in the years following drought could have been affected directly by reduced growth rates during leaf expansion, and indirectly through the effects of drought on the C balance, leading to depletion of non-structural carbohydrates (Le Dantec et al., 2000). Water stress during spring could also have limited the size and the number of leaves by reducing the leaf number per bud (Le Dantec et al., 2000). Based on a model of aspen LAI, Hogg (1999) concluded that the drought-induced reduction in annual carryover of total non-structural carbohydrates could result in the reduction of LAI following drought. Landhäusser and Liefers (2003) observed a 3% reduction in the dry weight of the branches in the crown of northern clonal *Populus tremuloides* attributable to the tapping of a carbohydrate reserve during leaf flush. Drought-induced depletion of that reserve could have reduced the number or quality of buds formed during autumn bud set in 2003 (Frewen et al., 2000) and could have reduced the number and size of leaves emerging at leaf flush.

### 3.2. Interannual variation in $E$ , $g_{sv}$ and $\alpha$

As a first step to understand the possible mechanisms by which drought could have affected the photosynthetic uptake of  $\text{CO}_2$  in the aspen stand, we considered the impact of water limitation in the soil profile on  $g_{sv}$ . The variation of  $\theta$  within the root zone can markedly affect variation of  $g_{sv}$  and  $g_{sc}$  (Oren et al., 1998; Rambal et al., 2003). If water is limiting, then  $\theta$  becomes the major control on  $E$  and will influence the ecosystem water balance (Kelliher et al., 1993). The variations of annual  $E$  ( $E_a$ ), growing season mean  $E$  ( $E_{gs}$ ),  $g_{sv}$  and  $\alpha$  during 1994–2005 are shown in Fig. 4.  $E_a$  varied interannually by as much as 48% of the mean for the complete record.  $E_{gs}$  varied in a similar way. In the first year of drought (2001),  $E_a$  rose above the pre-drought (1994–2000) mean, mainly because that year was

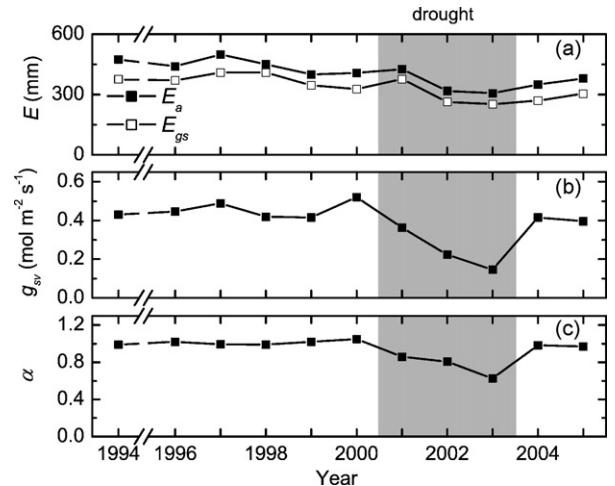


Fig. 4. Interannual variation in (a) annual ( $E_a$ ) and growing season ( $E_{gs}$ ) mean evapotranspiration, growing season mean values of (b) surface conductance ( $g_{sv}$ ) and (c) Priestley–Taylor coefficient ( $\alpha$ ) at SOA.

warmer and sunnier than average (Fig. 1) and  $\theta$  deep in the soil profile remained quite high (Fig. 2). As the drought progressed through 2002 into 2003,  $E_a$  dropped to its lowest value ( $p = 0.021$ , statistical significance obtained using the  $t$ -test) of the 11-year record ( $\sim 31\%$  lower than its pre-drought mean value). Both growing season mean  $g_{sv}$  and  $\alpha$  reached their lowest values in 2003 as they fell below their pre-drought mean values by  $\sim 70\%$  ( $p = 0.001$ ) and  $\sim 37\%$  ( $p < 0.001$ ), respectively.

Declines in the growing season averages of  $g_{sv}$  and  $\alpha$  tracked closely the declines observed in root zone water content—a finding consistent with Rambal et al. (2003), who observed a significant reduction of canopy conductance as a result of a 30% reduction in the relative water content ( $\theta/\theta_{FC}$ ) in the root-zone of a Mediterranean evergreen oak (*Quercus ilex*) stand. Granier et al. (2000) reported that canopy conductance of both coniferous and deciduous forests began to decline when the relative available water content dropped below 0.4. In our study, this occurred at the onset of the drought in 2001 when the root zone relative available water content fell below 0.65; similar declines in  $g_{sv}$  and  $\alpha$  were observed during the peak drought years of 2002 and 2003. In the 2 years following the drought,  $E_a$  increased significantly from its minimum values in 2002–2003 but remained below its pre-drought mean by  $\sim 21\%$  in 2004 and  $\sim 17\%$  in 2005, while  $g_{sv}$  and  $\alpha$  recovered to values close to their pre-drought means in 2004 and 2005. These are somewhat puzzling results, given that interannual variation in  $\alpha$  was well correlated with the variation in  $g_{sv}$  ( $r^2 = 0.88$ ),

emphasizing the role of stomatal control on  $E$ . We therefore attribute the low values of  $E$  in 2004 and 2005 mainly to the low levels of available energy in the growing season of those 2 years and also to the shortest canopy duration in 2004. Blanken et al. (1997) reported that the seasonal variation of  $g_{sv}$  at SOA was largely related to the aspen LAI, with the hazelnut understory contributing only  $\sim 24\%$  to the canopy  $g_{sv}$ . Aspen LAI remained 27 and 15% lower than its pre-drought mean in 2004 and 2005, respectively. Together, these results suggest that while  $E_a$  remained lower than pre-drought means, there was likely no lag in the recovery of transpiration rates following drought.

### 3.3. Interannual variation in annual $F_{NEP}$ , $P$ and $R$

#### 3.3.1. Annual $F_{NEP}$ , $P$ , $R$ and stem growth

Although SOA was a moderate C sink ( $F_{NEP} = 153 \pm 99 \text{ g C m}^{-2} \text{ year}^{-1}$ ) over the 11-year record, the annual  $F_{NEP}$  behaved differently as this ecosystem moved into, through and out of the drought period (2001–2003) (Fig. 5). In the first year of the drought, the depletion of water in the near-surface soil layer likely reduced soil respiration, and hence  $R$  (Fig. 5b), while water remaining deep in the soil column supported photosynthesis, resulting in above-average C uptake (Griffis et al., 2003; Kljun et al., in press; Barr et al., in press). In 2002 and 2003, the forest remained a moderate C sink because both  $P$  and  $R$  were much less than average. In 2004, annual  $P$  ( $1014 \text{ g C m}^{-2} \text{ year}^{-1}$ ) and  $R$  ( $1010 \text{ g C m}^{-2} \text{ year}^{-1}$ ) were 21 and 12%, respectively, below their pre-drought (excluding 1998) means ( $P = 1279 \pm 49$ ,  $R = 1146 \pm 41 \text{ g C m}^{-2}$

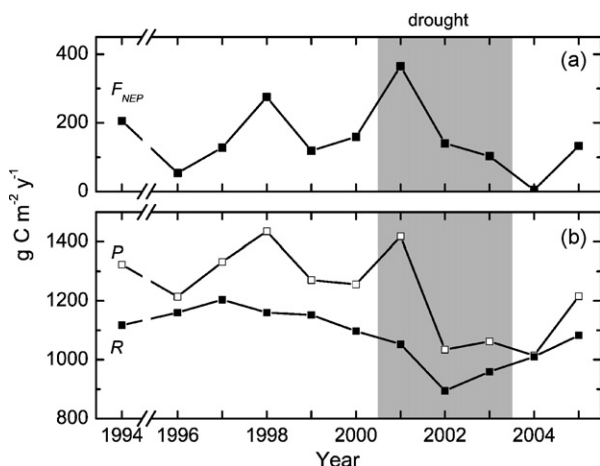


Fig. 5. (a and b) Interannual variation in net ecosystem productivity ( $F_{NEP}$ ), gross ecosystem photosynthesis ( $P$ ) and ecosystem respiration ( $R$ ) at SOA.

$\text{year}^{-1}$ ). We excluded 1998 because of the occurrence of a short drought early in its growing season (Barr et al., in press). The near-zero value of  $F_{NEP}$  in 2004 ( $4 \text{ g C m}^{-2} \text{ year}^{-1}$ ) resulted from a decrease in  $P$  and increase in  $R$  relative to their 2003 values. Although  $P$  ( $1216 \text{ g C m}^{-2} \text{ year}^{-1}$ ) and  $R$  ( $1083 \text{ g C m}^{-2} \text{ year}^{-1}$ ) were lower (by 5 and 6%, respectively) than their pre-drought means (excluding 1998)  $F_{NEP}$  in 2005 was the same as its pre-drought mean ( $F_{NEP} = 133 \pm 56 \text{ g C m}^{-2} \text{ year}^{-1}$ ) indicating the return of the aspen forest ecosystem to its pre-drought moderate C-sink status despite the below-average aspen LAI.

We examined the extent to which changes in annual  $F_{NEP}$  discussed above were reflected in direct measurements of ecosystem productivity by comparing annual daytime  $F_{NEP}$  ( $F_{NEPd}$ ) to stem growth during the years 1994–2004. The record of stem growth is shown together with the annual  $F_{NEPd}$  in Fig. 6. Here we considered  $F_{NEPd}$  because it represents the actual measured photosynthesis balanced by daytime respiration. Over the 11-year record, stem growth showed a better, positive correlation ( $r^2 = 0.56$ ) to annual  $F_{NEPd}$  than to the annual  $F_{NEP}$  ( $r^2 = 0.35$ ) (see Fig. 6a, inset), a consequence of the correlation between  $F_{NEPd}$  and  $P$  ( $r^2 = 0.58$ ) (see Fig. 5b). The estimated increment in mean stand basal area ranged from  $0.54$  to  $0.67 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$  in 1994–2000 while  $F_{NEPd}$  ranged from  $500$  to  $700 \text{ g C m}^{-2} \text{ year}^{-1}$ . In the first year of the drought (2001), annual  $F_{NEPd}$  ( $749 \text{ g C m}^{-2} \text{ year}^{-1}$ ) was above average, which corresponded to above-average stem growth ( $0.71 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$ ) in 2001. Below-average  $F_{NEPd}$  during the final 2 years of the drought (2002–2003) was accompanied by below-average stem growth ( $0.398$  and

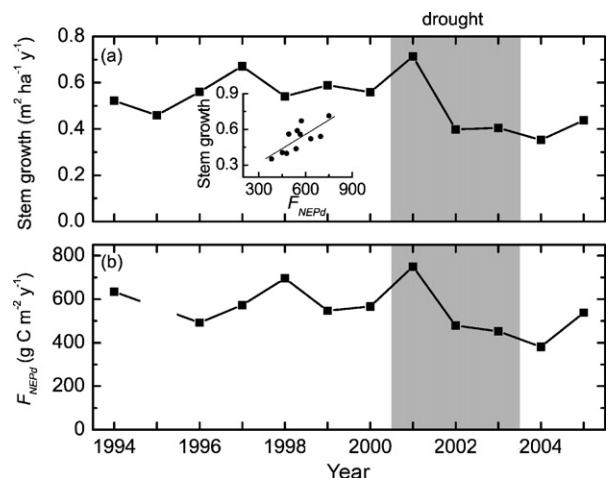


Fig. 6. Interannual variation in (a) stem growth and (b) annual daytime  $F_{NEP}$  ( $F_{NEPd}$ ) at SOA. The inset in (a) shows stem growth vs.  $F_{NEPd}$ .



0.405 m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>, respectively). The lowest  $F_{NEP}$  value of the 11-year record occurred in the first year following the drought (2004) and coincided with the lowest stem growth (0.352 m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>) of the record. The reduced stem growth and low full-leaf LAI (shown in Fig. 3) of the aspen indicate that its productivity declined during the 2002–2004 period. In 2005, stem growth showed evidence of partial recovery (average of 0.438 m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>), but was 25% lower than the pre-drought mean value (0.590 m<sup>2</sup> ha<sup>-1</sup> year<sup>-1</sup>).

### 3.3.2. Relationship of $P$ and $R$ to environmental variables

To determine what was expected given the environmental conditions, we considered simple relationships of  $P$  and  $R$  to environmental variables. Annual  $P$  and hence  $F_{NEP}$  at SOA is closely related to the spring temperature and hence earlier leaf emergence (Black et al., 2000; Barr et al., 2004). Earlier leaf emergence, results in significantly higher APAR during the growing season (Chen et al., 1999; Barr et al., 2004), which is shown in the high correlation between APAR and growing season length (GSL; days when  $F_{NEP} > 0$ ) (APAR = 45.4, GSL –1591 mol photons m<sup>-2</sup> year<sup>-1</sup>,  $r^2 = 0.89$ ,  $n = 11$ ). Fig. 7a shows that there is a good correlation between  $P$  and GSL for non-drought years (1994–2000, excluding 1998) ( $P = 12.36$ , GSL –112.9 g C m<sup>-2</sup> year<sup>-1</sup>,  $r^2 = 0.66$ ). As expected, in 1998 and 2001,  $P$  was slightly lower than that predicted from the non-drought relationship. As the drought progressed into 2002 and 2003, the annual  $P$  values observed were much lower than the values predicted by the relationship (Fig. 7a). In 2004,  $P$ , although showing significant recovery, remained lower than that predicted by the non-drought relationship, while agreement was improved in 2005.

$R$  is controlled by temperature (Goulden et al., 1996) and soil moisture (Griffis et al., 2004). The existence of a good correlation between annual  $R$  and  $T_s$  at the 2 cm depth in non-drought years ( $R = 60T_s + 430$  g C m<sup>-2</sup> year<sup>-1</sup>,  $r^2 = 0.75$  for years 1994–2000, excluding 1998) is clear from Fig. 7b. This analysis suggests that in 2001,  $R$  was slightly lower than that predicted from the relationship, while  $R$  in 1998 was very similar to the predicted value. With the progression of drought in 2002 and 2003,  $R$  dropped to values much lower than those predicted. In 2004, annual  $R$  was well above those of the peak drought years and was lower than that predicted by the relationship while in 2005,  $R$  was similar to the predicted value. Overall, the departures of observed  $P$  and  $R$  from their non-drought relationships with environmental variables highlight the fact that the

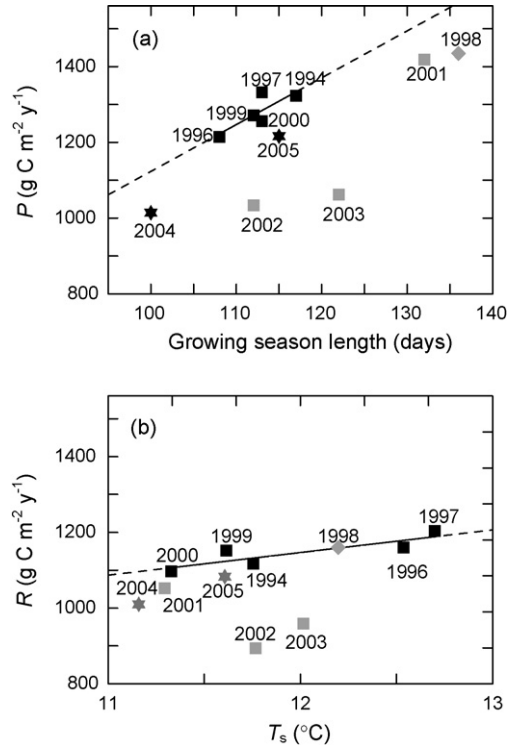


Fig. 7. (a) Gross ecosystem photosynthesis ( $P$ ) as a function of growing season length and (b)  $R$  as a function of growing season soil temperature at the 2 cm depth at SOA. The solid line in each panel represents the linear fit to data for 1994–2000, excluding 1998. Black and grey rectangles represent non-drought years (1994–2000) and drought years (2001–2003), respectively. The grey diamond represents the moderate drought year (1998) and the black stars represent the post-drought years (2004 and 2005).

near C-neutral status of SOA in 2004 was caused by the slower recovery of  $P$  compared to that of  $R$  following the end of the drought.  $P$  and  $R$  in 2004 were lower than predicted by the respective non-drought relationships by 109 and 87 g C m<sup>-2</sup> year<sup>-1</sup>, respectively, so that the actual  $F_{NEP}$  (4 g C m<sup>-2</sup> year<sup>-1</sup>) was less than the expected value by 22 g C m<sup>-2</sup> year<sup>-1</sup>.

### 3.3.3. Interannual variation of LUE and WUE

The adaptive response of the aspen trees is revealed in the interannual variation in LUE and WUE (Table 1). LUE decreased from the pre-drought mean of 0.029 mol C mol<sup>-1</sup> photons to 0.0260 mol C mol<sup>-1</sup> photons in 2001, which was likely the result of the high APAR values (~4550 mol m<sup>-2</sup>). LUE fell to 0.0257 in 2002 because low soil water content reduced  $P$ , with APAR decreasing to slightly below the 11-year average. In the final drought year (2003), above-average APAR coupled with the worst drought conditions resulted

Table 1

Interannual variation in growing season length, ratio of annual ecosystem respiration to gross ecosystem photosynthesis ( $R/P$ ), absorbed photosynthetically active radiation (APAR), ratio of APAR to PAR (FPAR), light use efficiency (LUE) and growing season water use efficiency (WUE)

Year	Growing season length <sup>a</sup> (days)	$R/P$	APAR (mol photons m <sup>-2</sup> year <sup>-1</sup> )	FPAR	LUE (mol C mol <sup>-1</sup> photons)	WUE (g C kg <sup>-1</sup> H <sub>2</sub> O)
1994	117	0.84	3816	0.454	0.0289	3.52
1996	108	0.96	3214	0.381	0.0315	3.28
1997	113	0.90	3828	0.448	0.0290	3.25
1998	136	0.81	4390	0.505	0.0272	3.51
1999	112	0.91	3712	0.453	0.0285	3.68
2000	113	0.87	3591	0.433	0.0291	3.83
2001	132	0.74	4550	0.506	0.0260	3.77
2002	112	0.86	3356	0.381	0.0257	3.92
2003	122	0.90	3858	0.446	0.0229	4.22
2004	100	0.99	2794	0.348	0.0302	3.75
2005	115	0.89	3552	0.432	0.0285	3.99
Mean ± S.D.	116 ± 10	0.88 ± 0.07	3696 ± 4965	0.435 ± 0.05	0.0263 ± 0.002	3.70 ± 0.30

<sup>a</sup> Growing season length refers to the days when 24 h  $F_{NEP} > 0$ .

in the lowest LUE ( $p < 0.01$ ) of the record (0.0229 mol C mol<sup>-1</sup> photons). Growing season mean of daytime atmospheric saturation vapor deficits ( $D$ ) increased during the drought years and in 2003 were ~35% higher than the pre-drought mean. The increase in  $D$  associated with the drought can impose severe limitations on the conversion efficiency of solar radiation into biomass by reducing the rate of photosynthesis and indirectly affecting the annual growth of trees (Runyon et al., 1994). LUE reached its highest value of the data record in 2004—the year immediately following the drought. The rapid recovery of LUE is likely the result of predominantly cloudy conditions and below-normal LAI values that produced, respectively, the lowest APAR and FPAR values of the 11-year record. Increases in the diffuse PAR fraction have been associated with concomitant increases in LUE (Turner et al., 2003; Still et al., 2004). In 2005, growing season LUE returned to values close to its pre-drought mean.

WUE showed a pattern opposite to that of LUE as it increased from the time of drought onset in 2001 and reached significantly higher values during the peak drought period of 2002–2003 ( $p = 0.022$ ) (Table 1). The observed increase in WUE with increasing drought stress and an associated reduction in  $g_{sv}$  are consistent with the results from earlier studies (Baldocchi, 1997; Williams et al., 1998). Although WUE is sensitive to both  $D$  and cloud cover (Williams et al., 1998; Rocha et al., 2004), the existence of a relationship between growing season WUE and  $D$  was not apparent in our study—a result consistent with observations made in deciduous forests by Law et al. (2002). In 2004, the

growing season WUE returned to a value close to its pre-drought mean. Interestingly, WUE increased to above-normal values in 2005 even though conditions at the site in that year were warm and wet. A striking ~18% increase in WUE (Table 1) was associated with a ~27% decrease observed in annual and growing season  $E$  during the 1994–2005 period, neglecting the drought years (Fig. 4a). Non-drought  $\alpha$  values remained fairly constant, suggesting the reduction in  $E$  likely resulted from a reduction in surface energy availability. During this period, mean downwelling short wave radiation (June–September) decreased by ~10%. In a recent review on the effect of warming climate on water availability in snow-dominated regions, Barnett et al. (2005) reported a decreasing trend in evapotranspiration for the last 50 years, which they attributed to a reduction in surface available energy due to increasing cloudiness and aerosol concentration. Increasing atmospheric CO<sub>2</sub> levels could also increase WUE through the increase in stomatal resistance (Policy et al., 1993; Nelson et al., 2004; Ainsworth and Long, 2005) and hence reduction in  $E$ , but a much longer SOA data record will be required to detect the presence of this effect.

### 3.4. Seasonal variation of $F_{NEP}$ , $P$ and $R$

#### 3.4.1. Analysis of the annual cycles of cumulative $F_{NEP}$

The preceding analysis suggests that an understanding of the mechanisms by which environmental factors affected ecosystem C exchange dynamics requires an inspection of the seasonal fluctuations of  $F_{NEP}$ ,  $P$  and  $R$ . To gauge the seasonal variation in the relative

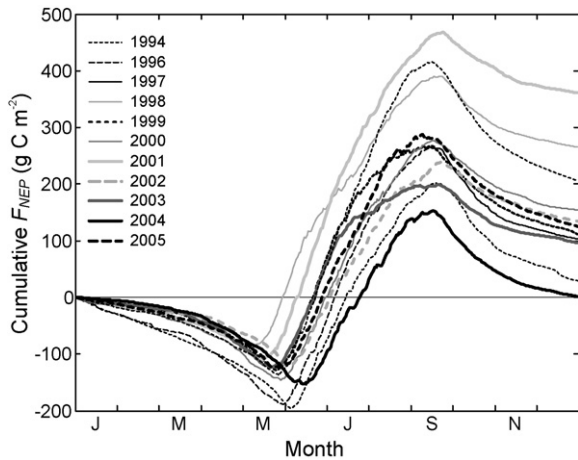


Fig. 8. Annual cycles of cumulative  $F_{NEP}$  at SOA.

magnitudes of  $P$  and  $R$  we analyzed the annual cycles of annual cumulative  $F_{NEP}$  for the entire data record (Fig. 8). We used 10-day average values of  $P$  (Fig. 9a),  $g_{sv}$  (Fig. 9b) and  $R$  (Fig. 10) to aid in our interpretation of the cumulative  $F_{NEP}$  plots for the pre-drought (1996 and 2000), drought (2001–2003) and post-drought (2004–2005) years. In order to assess post-drought recovery of  $F_{NEP}$ , we selected 1996, a year with a cold spring, and 2000, a year with a normal spring.

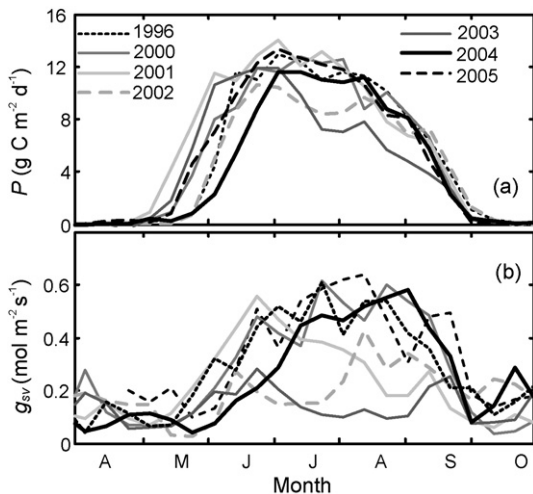


Fig. 9. Ten-day averages of (a)  $P$  and (b)  $g_{sv}$  from April to October at SOA for the 3 drought years, as well as for the year before (2000) and the 2 years after the drought (2004 and 2005). 1996 is included to show the pattern during a year with a cold spring like 2004, but with a wet growing season. Based on data from 2000 and 2003, the standard error of the 10-day mean values of  $P$  and  $g_{sv}$  for June, July and August typically varied from 0.18 to 0.89  $\text{g C m}^{-2} \text{day}^{-1}$  and 0.008–0.097  $\text{mol m}^{-2} \text{s}^{-1}$ , respectively.

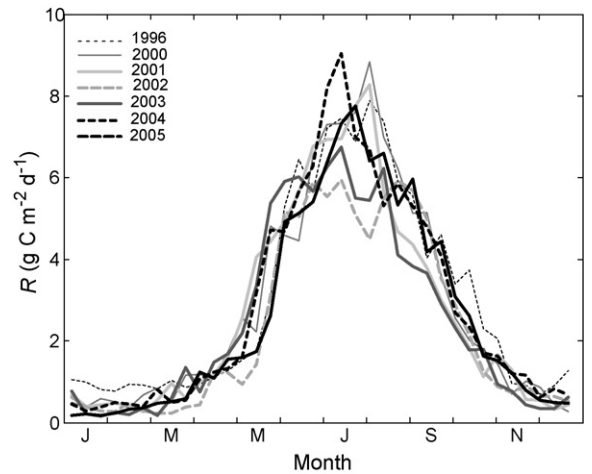


Fig. 10. Annual cycles of 10-day running mean of  $R$  for the same years as in Fig. 9 for SOA.

In general, the basic shape of the curve of cumulative  $F_{NEP}$  is the same for all years. The sharp increase in  $F_{NEP}$  in spring is associated with the occurrence of significant photosynthesis as a result of leaf emergence. The cumulative  $F_{NEP}$  plot suggests three reasons why the largest annual  $F_{NEP}$  was recorded in the first year of the drought. First, the ecosystem began sequestering C earlier than all other years (except in 1998), a direct consequence of the earliest onset of  $P$  in the data record (Fig. 9a). Next, the steep rise in the cumulative  $F_{NEP}$  curve indicated a large  $P$  to  $R$  ratio that took place over one of the longest growing seasons of the 11-year record (Table 1). With few exceptions, the 10-day means of  $P$  were among the highest from late April to the end of July in 2001, suggesting that the onset of the drought had little effect on  $P$ , despite the decline seen in  $g_{sv}$  throughout the growing season.  $P$  was likely supported by moisture replete conditions deeper in the soil profile, and was thus able to respond to the historically high levels of APAR (Table 1). Finally, the loss of C from the ecosystem toward the end of the year (2001), indicated by the slow descent of the curve after it had reached its maximum, was relatively small, because 10-day means of  $R$  were among the smallest in the record from mid-August to late October (Fig. 10). The heterotrophic component of  $R$  had already responded to the moisture deficit in the shallow soil layers (Griffis et al., 2004). Thus C dynamics during 2001 were determined by a time lag in the response of  $P$  compared to  $R$  to the onset of drought.

The annual  $F_{NEP}$  values for the peak drought years of 2002 and 2003 were similar to those of pre-drought years (Fig. 5). However, the cumulative  $F_{NEP}$  curves for these years are distinct from those of the pre-drought

years by virtue of their shape as they approach and descend from their maxima, suggesting that very different C dynamics were responsible for the annual total  $F_{\text{NEP}}$ . In 2002, the slope of the curve from mid-June to August is noticeably smaller than the pre-drought years and drops to a lower value between mid-August and September. For 2003, the rise of the curve to its maximum was interrupted prematurely in comparison to non-drought years: it began to level off in mid-July. Inspection of the 10-day average values of  $P$  (Fig. 9a), and  $R$  (Fig. 10) suggest that although both  $P$  and  $R$  were depressed from their pre-drought patterns, the departure of the  $F_{\text{NEP}}$  curve from its pre-drought seasonal pattern can be largely attributed to the behavior of  $P$ . Almost as soon as  $P$  reached its maximum value in late June 2003, it decreased rapidly to the lowest values observed in the record for the period of mid-July to mid-September. This trend corresponds to the rapid decline in  $g_{\text{sv}}$ , suggesting that stomatal control of  $P$  dominated in this period. The relatively high values of  $g_{\text{sv}}$  during August and September of 2002 were likely due to the relatively high  $\theta$  in the near surface soil layer resulting from the precipitation received during that period. This effect is also apparent from the increase in  $P$  and  $R$  shown in Figs. 9a and 10.

In the first year following the drought (2004), as indicated earlier annual  $F_{\text{NEP}}$  was close to zero. The cumulative  $F_{\text{NEP}}$  curve departs from the seasonal pre-drought pattern and the principal differences include (1) a minimum value that occurred later in the spring than in all other years, (2) a maximum that occurred earlier than all years except 2005, and (3) a more rapid decline from the maximum during the latter part of the year. The first of these features is the result of the latest start of photosynthesis in the 11-year record (Fig. 9a). Snowmelt occurred earlier in 2004 than in 2002, the year with coldest spring. However, the monthly mean air temperature in May 2004 was the lowest of the 11-year record and temperatures were also low in the first week of June. The growing season started in the second week of June, almost coinciding with the recharge of the soil water in the lower part of the soil profile (Fig. 2).  $g_{\text{sv}}$  increased from one of its lowest values in the record in late May and reached near pre-drought values in early July.  $P$  also reached pre-drought values in early July in spite of reduced LAI, in contrast to  $R$ , which reached pre-drought values in early June. The cumulative  $F_{\text{NEP}}$  maximum occurred slightly earlier in 2004—a consequence of early start of senescence in that year, possibly brought about by the cool weather. Senescence in 2005 was also slightly earlier than pre-drought years. The drought did not lead to earlier senescence during the peak drought period (Barr

et al., in press), as has been reported for a temperate forest ecosystem (Humphreys et al., 2005). Finally, the descent of the cumulative  $F_{\text{NEP}}$  curve from its 2004 maximum is relatively steep compared to the drought years of 2001–2003.  $R$ -values through the late growing season and early autumn were among the highest of the data record, a likely consequence of active heterotrophic respiration throughout the soil profile recently recharged with water. Earlier studies reported that the effect of the severe drought can spread over a period longer than the actual period of drought due to the rate of root turn over, partially non-reversible effects on canopy function such as inducing senescence effects (Reichstein et al., 2002), and xylem cavitation (Law et al., 2001; Addington et al., 2004).

The seasonal variation in cumulative  $F_{\text{NEP}}$  in 2005 fell between that in the non-drought years of 1999 and 2000. In general, the seasonal patterns of  $P$ ,  $R$ , and  $g_{\text{sv}}$  indicate that post-drought C dynamics have largely returned to those in pre-drought years. Barr et al. (in press) hypothesised that the build up of labile litter during drought or the stimulation of fine root growth following the drought would cause a transient, post-drought increase in  $R$  and hence a decline in  $F_{\text{NEP}}$ . There was no evidence of a transient, post-drought increase in  $R$  in 2004, and the high values of  $R$  in July 2005 were likely due to the warm and wet conditions (Fig. 10).

#### 3.4.2. Response of core growing season $P$ , $R$ , $\alpha$ and $g_{\text{sv}}$ to $\theta$

To examine the influence of increasing soil water deficits on  $P$ ,  $R$  and  $g_{\text{sv}}$ , during the growing season, we limited our analysis to the period starting 1 week after the minimum cumulative  $F_{\text{NEP}}$  and ending 2 weeks before the maximum value of cumulative  $F_{\text{NEP}}$ . This period, which we defined as the “core growing season” corresponds closely to the period when the forest is fully leafed. Core growing season values of  $P$ ,  $\alpha$ , and  $g_{\text{sv}}$  were plotted against average  $\theta$  in the 0–1.2 m soil profile over the core growing season for the entire 11-year data record (Fig. 11a). We used the average  $\theta$  in the 0–1.2 m soil profile because  $\theta$  throughout the root zone likely influences all three variables. The decline in root zone  $\theta$  below  $0.27 \text{ m}^3 \text{ m}^{-3}$  in 2002 and 2003 ( $\theta_{\text{RA}} \sim 0.8$ ) reduced the core growing season values of  $P$ ,  $\alpha$  and  $g_{\text{sv}}$ . In all other years, including 2004 and 2005,  $P$ ,  $\alpha$  and  $g_{\text{sv}}$  were almost independent of the variations in  $\theta$ . This supports our earlier hypothesis that it was the available water deep in the root zone that maintained photosynthesis immediately following the start of drought near its pre-drought levels. Persistent drought reduces long-term photosynthetic rates as soil water becomes

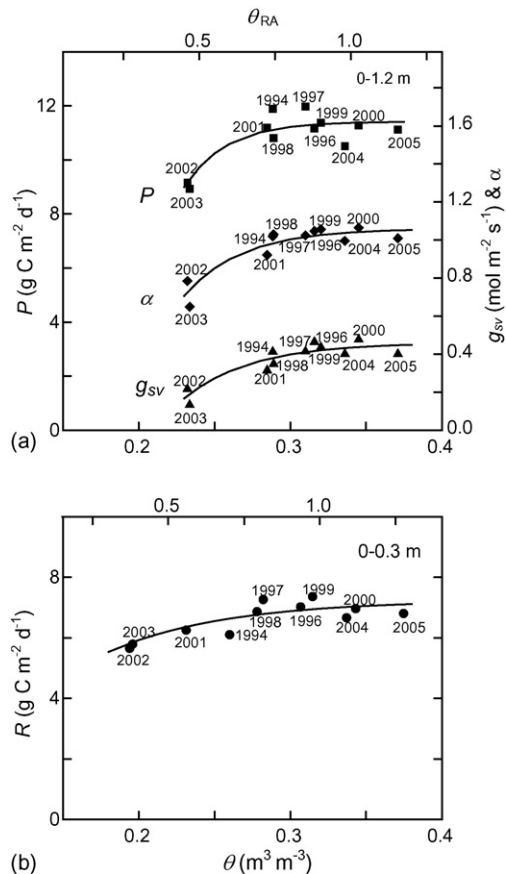


Fig. 11. (a) Core growing season mean  $P$ ,  $g_{sv}$  and  $\alpha$  as a function of average  $\theta$  in the 0–1.2 m soil profile at SOA and (b) core growing season mean  $R$  vs. average  $\theta$  in the 0–0.3 m layer. Solid curves represent non-linear fits to the data ( $y = a(1 - \exp(-bx)) + c$ ) with the coefficients  $a$ ,  $b$ ,  $c$  being 9323, 35.9,  $-9311.58$  ( $r^2 = 0.79$ ) for  $P$ , 151.62, 26.36,  $-150.56$  ( $r^2 = 0.87$ ) for  $\alpha$ , 50.48, 22.41,  $-50.02$  ( $r^2 = 0.83$ ) for  $g_{sv}$ , 17.42, 12.91,  $-10.18$  ( $r^2 = 0.75$ ) for  $R$ , respectively.

depleted in the root zone (Goulden et al., 1996; Reichstein et al., 2002; Griffis et al., 2004). The non-linear dependence of  $g_{sv}$  on  $\theta$  is similar to that reported by Oren et al. (1998) for a *Pinus taeda* forest and Rambal et al. (2003) for a Mediterranean evergreen oak *Quercus ilex* forest. For the range in  $\theta$  values observed over the pre- to post-drought period, core growing season  $P$  varied only by 24%, while that of  $g_{sv}$  varied by 75%. The existence of coupling between  $g_{sv}$  and the C assimilation process is well known (Law et al., 2000; Reichstein et al., 2002); however, the inference of  $g_{sv}$  as a primary control on  $P$  via the limitation of CO<sub>2</sub> supply is not straightforward (as discussed below). Unlike diffusion of water vapor out of the leaf, the diffusion of CO<sub>2</sub> molecules into the leaf to the sites of carboxylation responds to an additional series of internal gas and liquid phase resistances collectively termed the transfer

conductance (see Warren et al., 2003). Further, environmental stress may negatively affect  $P$  via suppression of the enzymatic activity of Rubisco.

The decline of core growing season mean  $R$  was noticeable when the  $\theta_{RA}$  dropped below 0.5 in the 0–0.3 m soil layer (Fig. 11b). Over the 11-year record, the interannual variation in core growing season  $R$  was independent of the core growing season mean soil temperature at the 0.02 m depth, which varied from 11 to 13 °C. The lowest value of  $R$  in 2002 and 2003 occurred when  $\theta_{RA}$  dropped to 0.3. In 2004 and 2005, core growing season mean of  $R$  was similar to those of pre-drought years, indicating the fast recovery of soil microbial activity following the recharging of soil water. The seasonal variation in  $R$  during 2001 (Fig. 10) suggests that the effects of decreased  $\theta$  in the shallow soil layers on  $R$  only became apparent later in the year. Over all,  $R$  was more sensitive to changes in  $\theta$  in the shallow layer of soil than  $P$ , while  $P$  was more sensitive than  $R$  to low values of  $\theta$  in the 0–1.2 m soil profile, similar to the findings of Barr et al. (in press).

The results from this study suggest that for the period considered here, the increase in  $F_{NEP}$  following drought onset (in 2001) and the decrease in  $F_{NEP}$  during (2002–2003) and following the drought (2004) offset each other. These opposing responses were brought about by a lag in the responses of  $P$  and  $R$  that was largely mediated by the water content of the upper (on  $R$ ) and lower (on  $P$ ) layers of the soil profile. The additional delay in the response of  $P$  to the recharge of the soil water may be due to the time required for recovery the leaf photosynthesis and normal functioning of stomata as evident from Fig. 9b. While the overall resilience of the ecosystem C balance in aspen forest to severe drought is apparent, physiological variables such as LAI showed only partial recovery even 2 years following the drought—a possible indication of the degree to which carbohydrate reserves in the crown branches were depleted during the drought period. The results of this study take on new importance in light of the forecast shift towards continental drying at mid-latitudes (IPCC, 2001) and the prediction of earlier snowmelts in the spring (Barnett et al., 2005). The question of whether ecosystem photosynthesis will always be able to overcome limitations such as a low post-drought LAI will be key to predicting the effects of longer drought periods on CO<sub>2</sub> exchange in this ecosystem.

#### 4. Conclusions

1. Above-average gains made in C sequestration ( $F_{NEP}$ ) in the first year of the drought were significantly

- offset by below-average stand  $F_{\text{NEP}}$  in the peak years of the drought and in the year following the drought.
2. Drought effects revealed in the interannual variations of  $F_{\text{NEP}}$  were also reflected in the annual measurements of stem growth, which were well correlated with those of  $P$  and daytime  $F_{\text{NEP}}$ . The drought significantly reduced full-leaf LAI and it remained lower than its pre-drought mean even 2 years after the drought.
  3. Ecosystem  $P$  was slower to respond to the onset and end of drought conditions than ecosystem  $R$ , an effect largely attributable to the control of  $P$  by the water content deep in the root zone and the control of  $R$  largely by the near surface soil water content.
  4. In the first year following the drought,  $F_{\text{NEP}}$  reached the lowest value of the record due to the combined effects of the shortest growing season, the lowest full-leaf LAI and the slower recovery of  $P$  compared to  $R$ , while in the second year following the drought,  $P$  returned to near to its pre-drought mean even though LAI remained less than its pre-drought mean, suggesting that aspen photosynthesis was able to adjust to this restriction on C assimilation.

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