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The sensitivity of carbon fluxes to spring warming and summer drought depends on plant functional type in boreal forest ecosystems

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Abstract

Warming during late winter and spring in recent decades has been credited with increasing high northern latitude CO_2 uptake, but it is unclear how different species and plant functional types contribute to this response. To address this, we measured net ecosystem exchange (NEE) at a deciduous broadleaf (aspen and willow) forest and an evergreen conifer (black spruce) forest in interior Alaska over a 3-year period. We partitioned NEE into gross primary production (GPP) and ecosystem respiration (R_e) components, assessing the impact of interannual climate variability on these fluxes during spring and summer. We found that interannual variability in both spring and summer NEE was greatest at the deciduous forest. Increases in spring air temperatures between 2002 and 2004 caused GPP to increase during the early part of the growing season (April, May, and June), with a 74% increase at the deciduous forest and a 16% increase at the evergreen forest. R_e increased in parallel, by 61% and 15%, respectively. In contrast, a summer drought during 2004 caused GPP during August to decrease by 12% at the deciduous forest and by 9% at the evergreen forest. Concurrent increases in R_e, by 21% and 2% for the two forests, further contributed to a reduction in net carbon uptake during the drought. Over the growing season (April–September) net carbon uptake increased by 40% at the deciduous forest and 3% at the evergreen forest in 2004 as compared with 2002. These results suggest that deciduous forests may contribute disproportionately to variability in atmospheric CO_2 concentrations within the northern hemisphere and that the carbon balance of deciduous forests may have a greater sensitivity to future changes in climate.
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Keywords: *Populus tremuloides*; *Picea mariana*; Arctic and boreal ecosystems; Carbon cycle; Eddy covariance; Global warming

1. Introduction

From the 1970s to 2005, surface air temperatures in arctic and boreal biomes increased by approximately 0.4 °C per decade (ACIA, 2004; Hansen et al., 2006). The consequence of these temperature increases, and further increases predicted over the next several decades (IPCC, 2001), for carbon stores in northern ecosystems remains uncertain because temperature changes may trigger both positive and negative feedbacks with the carbon cycle (Braswell et al., 1997; McGuire et al., 2006).

In northern forests, there are multiple competing effects of increasing air temperatures on gross primary productivity (GPP) and ecosystem respiration (R_e). Warmer springs lead to an earlier onset of photosynthesis (Black et al., 2000; Tanja et al., 2003), enhance GPP during spring months (Goulden et al., 1996; Arain et al., 2002; Angert et al., 2005) and often increase annual net

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carbon uptake (Chen et al., 1999; Black et al., 2000; Barr et al., 2002; Chen et al., 2006). However, increased temperatures can also increase the depth of soil thaw (Euskirchen et al., 2006), exposing more soil organic matter to decomposition (Goulden et al., 1998; Hirsch et al., 2002) and causing a net loss of carbon from ecosystems (Goulden et al., 1998; Lindroth et al., 1998; Valentini et al., 2000).

Low moisture conditions during drought (created by either anomalously low precipitation or anomalously high temperature that increases evapotranspiration) cause both GPP and R_e to decline (Ciais et al., 2005; Kljun et al., 2006). There is still debate about whether GPP or R_e is most adversely affected by drought and thus the sign of the net ecosystem exchange (NEE) response in different ecosystems. An extreme drought in Europe during 2003, for example, caused many ecosystems to lose carbon (Ciais et al., 2005). In contrast, Goulden et al. (1996) found that R_e was more sensitive to reduced soil moisture availability than GPP, and this caused carbon to accumulate at a faster rate during a late-summer drought in a temperate deciduous forest. Similarly, decreases in soil respiration from limited moisture availability causes net ecosystem carbon uptake to increase during the dry season in moist tropical forest ecosystems (Saleska et al., 2003). The net effect of drought may depend on the severity of moisture limitation. Reichstein et al. (2002) hypothesize that during conditions where only the surface soil layers are affected, heterotrophic R_e will be impacted more than GPP (increasing net carbon uptake) and that it is not until severe drought conditions substantially lower the water table that GPP will be affected adversely through plant water stress.

Physiological and phenological differences between deciduous and coniferous forests (e.g., Falge et al., 2002) are likely to modulate the response of these two forests to climate variability. Monson et al. (2005), for example, propose that the annual carbon balance of deciduous forests is limited by the fraction of the year that leaves are still expanding and have not reached maximum leaf area. This fraction is reduced in years with early spring leaf-out, thereby increasing GPP. In contrast, the annual carbon balance of evergreen conifers may be regulated more strongly by a reduction in GPP caused by mid-summer drought stress which typically increases in years with earlier springs as a result of earlier snowmelt and surface runoff (Monson et al., 2005).

Interannual eddy covariance measurements in the boreal zone show that warm springs increase GPP substantially in deciduous aspen forests and to a lesser degree in evergreen black spruce forests (Black et al., 2000; Arain et al., 2002). During warm summers, in the absence of drought, deciduous aspen forest R_e remains largely unchanged (Arain et al., 2002; Griffis et al., 2003; Kljun et al., 2006), whereas evergreen black spruce R_e increases substantially (Goulden et al., 1998; Arain et al., 2002). Therefore, warm years appear to increase annual net carbon uptake in aspen forests (Black et al., 2000; Arain et al., 2002), and may decrease annual net carbon uptake in black spruce forests (Goulden et al., 1998). Kljun et al. (2006) found that higher soil moisture contents due to inherently low soil drainage at an evergreen black spruce forest buffered the effect of drought compared with that in a nearby drier deciduous aspen forest with higher rates of soil drainage.

Here, we report measurements of NEE at a deciduous aspen forest and an evergreen black spruce forest over 3 years (2002–2004) in interior Alaska. Our objective was to determine how plant functional type (deciduous versus evergreen) modulates ecosystem carbon flux response to interannual climate variability. These two forests were part of a fire chronosequence that has been used in the past to examine the effects of post-fire stand age on the soil microbial community (Treseder et al., 2004), variability in burn severity (Kasischke and Johnstone, 2005), surface energy fluxes (Liu et al., 2005), and the seasonal cycle of atmospheric CO_2 and $\delta^{18}O$-CO_2 (Welp et al., 2006). Spring air temperatures increased progressively during 2002 through 2004. The summer of 2004 was one of the hottest and driest in Alaska (ACRC, 2006), contributing to the worst fire season on record (AGDC, 2006). Because of the close proximity of the sites to one another, it was possible to directly compare the relative effects of the same climate variability on net carbon uptake in two different forest types. We found that the deciduous aspen forest was much more sensitive to variability in climate than the evergreen black spruce forest.

2. Methods

2.1. Site description

We measured NEE using the eddy covariance technique at two forests in interior Alaska near Delta Junction (63°54′N, 145°40′W). One had an overstory primarily comprised of *Picea mariana* (black spruce) and is hereafter referred to as the evergreen conifer forest. Understory species at this site in 2002 included *Vaccinium uliginosum*, *Vaccinium vitisidaea*, *Betula*

glandulosa, and *Ledum palustre*. Dominant mosses included *Hylocomium splendens* and *Pleurozium schreberi*. Lichens within the moss layer included *Cetraria* spp., *Cladonia* spp., *Cladina* spp. and *Peltigera* spp. (Mack et al., submitted). The thickness of the organic soil layer in this forest was approximately 10.5 cm (Manies et al., 2001; Neff et al., 2005). Field measurements from 2003 show that the fraction of photosynthetically active radiation (FPAR) remained relatively constant from mid-May through June, and then increased from July through September as solar zenith angles increased (Steinberg et al., 2006).

A second forest, separated by a distance of ~17.5 km from the evergreen conifer forest, had an overstory comprised primarily of *Populus tremuloides* (aspen) and is hereafter referred to as the deciduous broadleaf forest. *Salix* spp. (willow shrubs) contributed substantially to understory net primary production and biomass during a 2002 harvest (Mack et al., submitted). Other abundant understory vascular plants included *Epilobium angustifolium* and *Festuca altaica*. A thin layer of mosses (*Politrichum* spp.) covered some of the exposed soil surfaces. The thickness of the organic soil layer here was approximately 5.4 cm, half of that of the evergreen conifer forest (Manies et al., 2001). FPAR measured in 2003 increased substantially from mid-May to mid-June, and measurements from 2002 were relatively constant from mid-June through August and decreased rapidly in September (Steinberg et al., 2006).

Mineral soils in this area are well-drained with approximately 30 cm of loess covering a moraine gravel layer (Manies et al., 2004; Neff et al., 2005). Permafrost does not appear to be present at our two sites even though they are within a region of Alaska characterized by discontinuous permafrost (Harden et al., 2006).

Within interior Alaska and in northern Canada, fire is a primary disturbance agent that influences species composition and the distribution of stand ages at a regional scale. Most fires are stand replacing – killing almost all of the overstory trees and consuming varying degrees of the soil organic layer. Post fire successional trajectories may include a broadleaf deciduous phase (e.g. *Populus tremuloides*) in areas that are dry and well-drained (Viereck et al., 1983) or where much of the soil organic layer is consumed (Johnstone and Kasischke, 2005). In this context, it is worth noting that our two sites were in varying stages of recovery from fire-induced disturbance. The deciduous broadleaf site burned during the summer of 1987 in the Granite Creek fire and thus had a stand age of 15 years in 2002 (AGDC, 2006). The evergreen conifer forest had a stand age of ~80 years, based on an analysis of tree rings at the site.

As a result of their differing ages, the two stands were probably accumulating carbon at different rates (e.g., O'Neill et al., 2003; Randerson et al., 2006). Concurrent changes in the canopy overstory and the build up of the soil organic layer decreased soil temperatures during spring and summer at the evergreen conifer forest (Liu et al., 2005) with consequences for ecosystem processes, including decomposition and nutrient availability (Treseder et al., 2004). The coupling between post-fire succession and forest type may influence some of the results presented in Section 3. For example, a small component of the 2002 to 2004 increase in growing season net flux observed at the deciduous broadleaf forest may have been caused by a small secular increase in leaf and sapwood area.

2.2. Measurement and analysis approach

Eddy covariance towers were equipped with open-path infrared gas analyzers (IRGA's) (LI-7500, LI-COR, Inc., Lincoln, Nebraska) and sonic anemometers (CSAT3, Campbell Scientific, Inc., Logan, Utah). Instrument heights and configurations are summarized in Liu et al. (2005). Briefly, air temperature and relative humidity were measured at three heights at each site with temperature/humidity probes (HMP45C, Vaisala, Inc., Helsinki, Finland). Above canopy photosynthetic photon flux density (PPFD) was measured using LI-190 sensors (LI-COR, Inc.). Soil moisture was measured by TDR soil moisture sensors (CS615, Campbell Scientific, Inc.) installed at four depths (at 2, 5, 22, and 27 cm at the evergreen forest and at 2, 4, 11, and 37 cm at the deciduous forest). Atmospheric pressure (CS105, Vaisala, Inc.) was used with air temperature and relative humidity measurements to calculate vapor pressure deficit (VPD).

The sonic anemometer and the IRGA output were recorded by dataloggers (CR5000, Campbell Scientific, Inc.) at 10 Hz. Fluxes of sensible heat, latent heat, and CO_2 were calculated using the 30-min covariance of vertical wind velocity and virtual temperature, water vapor density, and CO_2 density. We calculated sensible heat fluxes from buoyancy fluxes derived from the sonic temperature as described by Campbell Scientific CSAT3 documentation (most recently updated 2/07) and Schotanus et al. (1983). CO_2 fluxes obtained from the open-path IRGA were corrected for density effects following the approach described by Webb et al. (1980).

CO_2 calibrations were performed using a CO_2 in compressed air reference tank as a span gas and using a soda lime scrub to remove CO_2 from this standard for the zero gas. Water vapor calibrations were made using

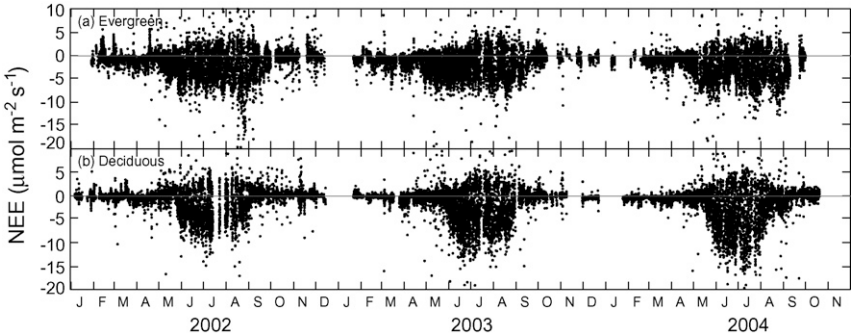

Fig. 1. Thirty-minute mean NEE measurements from 2002–2004 for the (a) evergreen and (b) deciduous forests. Positive values represent a release of CO_2 from the ecosystem into the atmosphere and negative values denote uptake of CO_2 by the ecosystem. (For comparison with the other figures, 1.0 μmol m^{-2} s^{-1} equals 1.04 g C m^{-2} day^{-1}.)

compressed air with a magnesium perchlorate desiccant as a zero gas and output from a dew point hygrometer (model LI-610, LI-COR, Inc.) during the fall of 2001 when the two towers were installed. During the summers of 2002, 2003, and 2004, the water vapor span was estimated using the dew point measurements from recently calibrated Vaisala temperature/humidity probes at the same height as the IRGA. Internal desiccant and soda lime bottles within the LI-7500 were replaced at 6-month intervals. Half hour fluxes were rejected when the time-series data points were less than 50% of the full length (i.e., 18,000 points). We did not find any statistically significant relationship between wind direction and surface energy budget closure for our sites and thus we included data from all wind directions in our analysis.

We further filtered NEE measurements using a u_* threshold of 0.2 m s^{-1} (Goulden et al., 1997). We applied a threshold based on the automatic gain control (AGC) of the optical path of the LI-7500 to remove periods of water, dust, and aerosol deposition that interfered with the LI-7500 optics. The AGC thresholds we used were specific to each IRGA. During the summer of 2004, fires in the region caused a layer of aerosol to deposit on the LI-7500 open-path sensors at both sites from 4 July until a calibration visit on 28 July. This caused CO_2 concentrations to decrease by up to 5% at the evergreen forest and by 6% at the deciduous forest. For this period of aerosol contamination, 10 Hz CO_2 concentrations were adjusted by a linear scalar so that daily mean CO_2 levels in 2004 were similar to measurements during this period in 2003, thus accounting for the large seasonal swing in CO_2 that occurs during July within interior Alaska. Considering all missing and rejected NEE data including those previously mentioned and also temporary interruptions from power loss and equipment malfunction, the percent availability of 30-min mean NEE observations during April–September of 2002, 2003 and 2004 was 47%, 60%, and 54% at the deciduous forest and 56%, 59%, and 50% at the evergreen forest.

We confined our analysis to the April to September period to optimize the signal to noise ratio of the open-path LI-7500 IRGA. Radiation absorption and heat dissipation by the instrument may create local air density anomalies that influence CO_2 column abundance within the instrument optical path (Amiro et al., 2006a; Burba et al., 2006). These anomalies are challenging to quantify and may be larger during winter months, contributing to the apparent negative CO_2 fluxes measured during cold winter months (e.g., Fig. 1 of this paper and Figs. 1 and 3 of Amiro et al. (2006a)). We estimated, using the flux partitioning model described below, that the 1 April–30 September period accounted for over 97% of the total annual GPP at both the deciduous and evergreen forests.

Gaps in the growing season NEE observations were filled with modeled NEE using measured microclimate variables as drivers of R_e and GPP models. In the case of each of the carbon fluxes reported here, positive values represent a source to the atmosphere and negative values represent uptake by the ecosystem.

$$\mathrm{NEE} = R_e + \mathrm{GPP} \quad (1)$$

A detailed description of the approach used to model R_e and GPP is given by Welp et al. (2006). Briefly, daytime and nighttime R_e during periods of missing data were estimated from a temperature dependent Q_{10} respiration model. The temperature sensitivity (the Q_{10} value) was solved using growing season (April–September) nighttime NEE measurements and 10 cm soil temperatures from the 3 years of combined data. Baseline respiration rates (at 10 °C) for each forest were solved for using 15-day intervals moving by 5-day increments during the

growing season allowing the R_e model to respond to seasonal changes in substrate availability and soil moisture.

GPP was estimated by subtracting R_e from available daytime NEE observations. During daytime periods of missing NEE observations, GPP was modeled as a function of photosynthetic photon flux density (PPFD), the fraction of absorbed photosynthetically active radiation (FPAR), quantum efficiency, and a maximum photosynthetic uptake rate using a Michaeles–Menton model. FPAR and leaf area index (LAI) were obtained from the MODerate Resolution Imaging Spectroradiometer (MODIS) satellite (Myneni et al., 1997; Myneni et al., 2002; ORNL, 2007). Additionally, a vapor pressure deficit (VPD) scalar was used in the GPP model to capture reductions in GPP associated with decreases in stomatal conductance during high VPD conditions (Welp et al., 2006). The GPP model solved for quantum efficiencies and maximum photosynthetic uptake rates every 7-days by using measured PPFD and tuning these model parameters to the available GPP data during that interval. Therefore, the model captured week-to-week variability in NEE response to environmental conditions such as temperature and moisture stress at each forest in addition to light intensity (i.e., PPFD). The onset of the growing season for each forest was defined as the day which the gap-filled sum of daily NEE became negative (indicating net uptake of CO_2 by the ecosystem on that day) and stayed negative for at least three consecutive days. The end of the growing season was defined in a similar manner, when daily NEE became positive for at least three consecutive days in August or September with no subsequent sustained 3-day period of negative daily NEE.

3. Results and discussion

3.1. Mean seasonality of ecosystem carbon fluxes

Eddy covariance NEE measurements at each of the two forests from 2002 through 2004 are presented in Fig. 1. The period of carbon accumulation was shorter and more intense at the deciduous forest than at the evergreen forest (Fig. 1). The mean interval of net carbon accumulation, defined as the continuous period when daily total NEE was negative, was 100 days at the deciduous forest (from 23 May through 31 August) and 144 days at the evergreen forest (from 21 April through 12 September) (Fig. 2).

Gap-filled NEE measurements (at a 30-min temporal resolution) were used to construct weekly mean NEE fluxes and are presented along with estimates of GPP

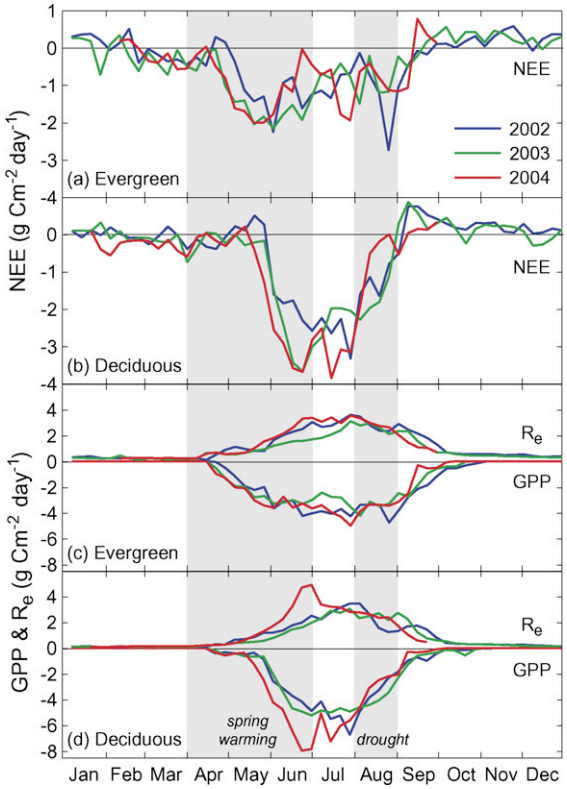

Fig. 2. Weekly mean NEE, GPP and R_e for the evergreen and deciduous forest sites. Positive values in panels (c) and (d) are R_e fluxes to the atmosphere and negative values are GPP uptake by the forests. Spring temperatures increased from 2002 through 2004 and a severe drought occurred during August of 2004 (shaded intervals).

and R_e derived from our flux-partitioning model in Fig. 2. During June and July, mean daily NEE at the deciduous forest, averaged over the 3 years of measurements, was -2.7 ± 0.4 g C m^{-2} day^{-1} (error represents the range of values for individual years) and was two to three times larger than that measured at the evergreen forest, -1.0 ± 0.1 g C m^{-2} day^{-1}. Arain et al. (2002) reported a similar factor (greater than 2) for the difference between the same two forest types in central Canada. Over 95% of annual GPP at the deciduous forest occurred over the 119-day interval between 14 May and 9 September. In contrast, photosynthetic activity was 29 days longer at the evergreen forest, with 95% of GPP distributed over the 27 April through 21 September period.

Averaged over the 3 years, maximum carbon uptake at the evergreen forest occurred during late May and early June. From mid-June through early August, there was a decline in net carbon uptake observed at the evergreen forest that was not seen at the deciduous forest (Fig. 2). This pattern has been previously reported

for black spruce in Canada and was attributed to seasonal differences in the relative rates of R_e and GPP (Goulden et al., 1998; Arain et al., 2002; Griffis et al., 2003; Dunn et al., 2006). From late May through late July at the evergreen forest, R_e increased substantially while GPP remained fairly constant (Fig. 2c), resulting in a decrease in net carbon uptake. Maximum R_e rates at the evergreen site corresponded to the mid-season July minimum in net carbon uptake. Evergreen GPP fluxes remained relatively constant at near maximum levels from late June through late August (Fig. 2c). In August, of 2002, a decrease in R_e and small increase in GPP caused a brief late-season increase in net carbon uptake.

In the deciduous forest, rates of net carbon uptake were highest during June and July (Fig. 2), and corresponded to the time of maximum LAI (Fig. 3). The periods of greatest carbon loss at the deciduous forest occurred during May and September (Fig. 2). During May, autotrophic respiratory fluxes were probably high as a result of tissue synthesis associated with budbreak and leafout (Ryan et al., 1994; Ryan et al., 1997). In contrast, during the September soil respiration may have persisted while soils were still warm, well beyond the time that leaf senescence and cold air temperatures shut down GPP (Russell and Voroney, 1998; O'Neill et al., 2003). During these transitional periods, GPP is less than R_e and this leads to net carbon release from deciduous forests during the edges of the growing season (Falge et al., 2002; Amiro et al., 2006b).

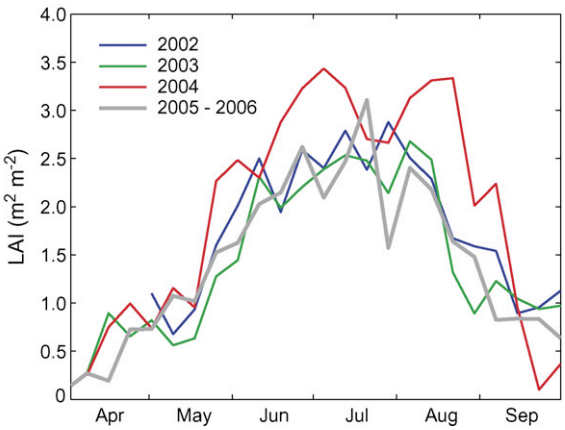

Fig. 3. Eight-day composite values of leaf area index (LAI) from Terra and Aqua MODIS at the deciduous broadleaf forest. The mean of all available QA filtered Terra and Aqua measurements (collection four of MOD15A2 and MYD15A2) are shown here for a 3 km × 3 km tile centered on the eddy covariance tower for 2002 through 2004. The mean LAI during 2005 and 2006 was lower than 2004, suggesting that the increase in LAI during 2004 was primarily linked with climate, rather than a secular trend caused by stand regrowth. Mean LAI values during May and June were 1.7, 1.4 and 2.0 $m^2\ m^{-2}$ for 2002, 2003 and 2004 respectively. Likewise the mean LAI values for July through August were 2.3, 2.1 and 3.0 $m^2\ m^{-2}$ respectively.

Differences in seasonal chlorophyll content of aspen and black spruce measured by Middleton et al. (1997) may help explain differences in seasonal GPP and hence NEE between forests. Higher chlorophyll content is directly correlated with increased photosynthetic capacity through increased light use efficiency (Field and Mooney, 1986). Middleton et al. (1997) found an early (late-May to early-June) and late (mid-September) peak in chlorophyll content in spruce whereas the aspen forest chlorophyll peaked only once during late-July through early-August (Middleton et al., 1997; Griffis et al., 2003). These seasonal patterns in chlorophyll are not identical to the seasonal GPP variability observed at the deciduous and evergreen forests in this study; however, they suggest that photosynthetic uptake may be enhanced in the spring and fall at the evergreen forest and during the mid-summer at the deciduous forest.

3.2. Early season warming

Interior Alaska experienced considerable interannual spring climate variability during 2002–2004 (Table 1 and Fig. 4). For this analysis we defined the spring period as April through June to capture a larger fraction of ecosystem fluxes during the early part of the growing season. Air temperatures increased progressively during the springs of 2002, 2003, and 2004 (Fig. 4a and Table 2). Spring soil moisture in 2002 was intermediate, 2003 was dry, and 2004 was wet due to differences in the amount of winter snow accumulation, spring rain, and soil thaw (Fig. 4c–f and Table 2).

Air temperature rather than radiation determines the start of the growing season in northern ecosystems (Jarvis et al., 1997; Baldocchi et al., 2000; Black et al., 2000; Jarvis and Linder, 2000; Arain et al., 2002; Tanja et al., 2003). The onset of the growing season for each year of measurement, defined by the first continuous 3-day period of net carbon uptake, was May 26, 2002, May 23, 2003, and May 17, 2004 at the deciduous forest and May 1, 2002, April 22, 2003, and April 17, 2004 at the evergreen forest. In the deciduous forest, weekly photographs and visit reports from the site confirmed the onset of the growing season occurred approximately within 1 week after aspen bud break. The onset of deciduous carbon uptake corresponded to LAI values of 1.6, 1.3 and 1.0 $m^2\ m^{-2}$ for each year respectively. From 2002 to 2004, the onset of the growing season advanced by 9 days at the deciduous forest and 14 days at the evergreen forest. Considerable variability in the onset of GPP is not unusual for deciduous and evergreen

Table 1
Climate data from nearby Big Delta, Alaska climate station[a]

	Record													
	January	February	March	April	May	June	July	August	September	October	November	December	Annual	April–September[b]
Precipitation (mm)														
Climate norm[c]	8.1	7.9	6.4	6.1	22.4	57.4	67.1	50.3	27.7	15.7	11.7	9.1	289.8	230.9
2002	1.3	0.0	4.1	14.5	12.2	75.9	52.3	89.4	32.0	15.7	4.8	3.3	305.6	276.4
2003	0.3	0.0	2.3	0.8	8.1	7.9	92.2	43.9	32.8	1.8	7.9	2.0	199.9	185.7
2004	2.3	1.5	2.0	3.3	42.7	30.7	39.1	23.1	20.6	14.5	5.1	9.9	194.8	159.5
Difference from climate norm														
2002	−6.9	−7.9	−2.3	8.4	−10.2	18.5	−14.7	39.1	4.3	0.0	−6.9	−5.8	15.7	45.5
2003	−7.9	−7.9	−4.1	−5.3	−14.2	−49.5	25.1	−6.3	5.1	−14.0	−3.8	−7.1	−89.9	−45.2
2004	−5.8	−6.4	−4.3	−2.8	20.3	−26.7	−27.9	−27.2	−7.1	−1.3	−6.6	0.8	−95.0	−71.4
Temperature (°C)														
Climate norm	−19.6	−15.6	−10.6	−0.7	8.3	14.1	15.6	12.9	6.6	−3.8	−13.8	−18.7	−2.1	9.5
2002	−12.1	−13.0	−11.5	−4.8	9.0	13.6	15.3	11.7	7.6	1.0	−3.8	−11.8	0.1	8.7
2003	−14.4	−7.0	−12.0	0.4	7.6	14.7	15.3	12.9	3.9	0.8	−13.4	−18.4	−0.8	9.1
2004	−24.1	−10.3	−13.0	2.5	10.5	18.0	17.5	16.1	2.8	−1.9	−9.1	−14.9	−0.5	11.2
Difference from climate norm														
2002	7.5	2.5	−0.9	−4.1	0.6	−0.5	−0.3	−1.2	1.0	4.8	10.0	6.9	2.2	−0.7
2003	5.2	8.6	−1.4	1.1	−0.7	0.6	−0.2	0.0	−2.7	4.5	0.4	0.3	1.3	−0.3
2004	−4.5	5.2	−2.4	3.2	2.2	4.0	1.9	3.2	−3.8	1.9	4.7	3.7	1.6	1.8

[a] Western Regional Climate Center (WRCC, 2006).
[b] April–September sum of precipitation and mean monthly temperature.
[c] Climate norm consisted of the mean from 1937–2005.

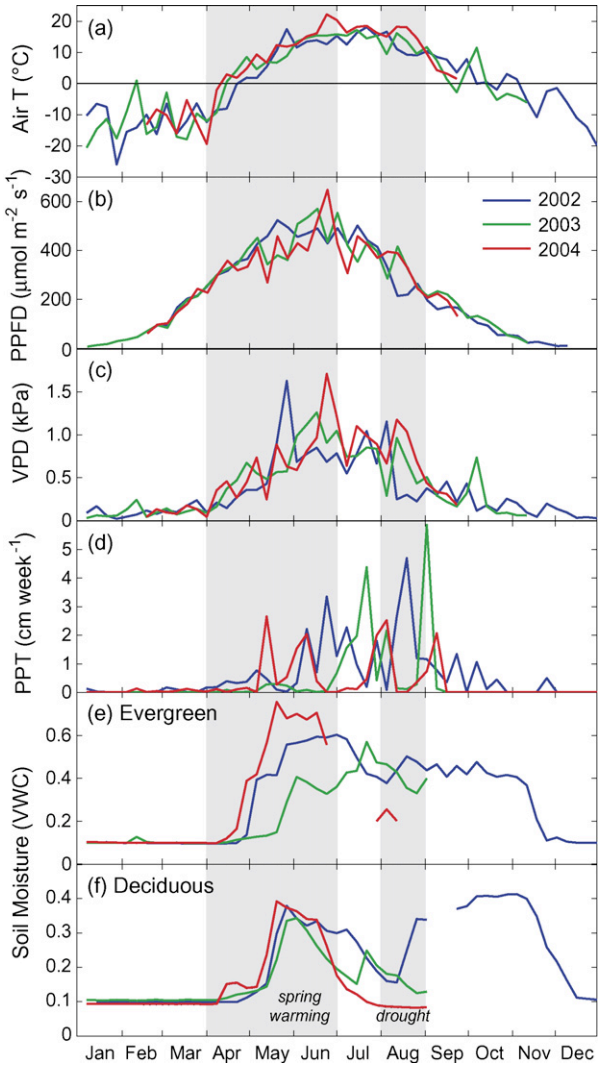

Fig. 4. Weekly mean climate conditions. (a) Air temperature measured above the canopy, (b) 24 h mean photosynthetic photon flux density (PPFD), (c) vapor pressure deficit (VPD) calculated from temperature and relative humidity measurements above the deciduous and evergreen canopies (mean of the two), (d) precipitation measured at the nearby Big Delta, Alaska climate station and distributed by week according to tipping bucket measurements at the deciduous forest (this figure does not represent continuous precipitation, but rather weekly sums) (e and f) volumetric water content (VWC) measured at (e) 22 cm at the evergreen forest (TDR measurements are equal to 0.1 when the soil is frozen) and (f) 11 cm at the deciduous forest.

forests (Black et al., 2000; Barr et al., 2002; Suni et al., 2003). Both the mean delay in the onset of the growing season at the deciduous forest compared to the evergreen forest (and the reduced sensitivity of the onset of photosynthesis to climate variability) may be linked with evolutionary strategies to avoid damage to newly formed leaves by spring frost events (Cannell and Smith, 1986). Low transpiration rates may also allow evergreen trees more flexibility in the initiation of GPP because black spruce trees, for example, can use water stored in sapwood for transpiration for several weeks during spring before the soil thaws (Tanja et al., 2003).

At both forests, spring photosynthetic uptake responded positively to increased air temperatures (Table 2). The increase in photosynthetic uptake (more negative GPP values) in the spring of 2004, during which air temperatures were 3.5 °C warmer and soil temperatures were 1.7 °C warmer than the spring of 2002, was substantially greater at the deciduous forest (74%) than the evergreen forest (16%). Although air temperatures in the spring of 2003 were 1.3 °C warmer than in 2002, there was less of an increase in photosynthetic uptake (increasing by 9% and 5% at the deciduous and evergreen forests, respectively, relative to 2002), perhaps because spring soil temperatures did not substantially change.

Soil moisture appeared to have a strong control on spring R_e, and caused a decrease in R_e at both sites during the relatively dry spring of 2003 (Table 2). Although the R_e model did not explicitly include moisture inputs, low moisture effects were captured because the baseline R_e rate was solved for using nighttime observations from 15-day moving intervals. If measured nighttime NEE (or R_e) fluxes decreased during dry periods, the baseline R_e in the model decreased. Warm and wet conditions during spring 2004 increased R_e at both sites, but had a larger effect on R_e at the deciduous forest (a 61% increase relative to 2002 as compared with a 15% increase at the evergreen forest).

Spring warming is predicted to increase forest productivity in northern ecosystems (White et al., 1999; Arain et al., 2002; Kimball et al., 2006). We found that the year-to-year variations in spring NEE at the deciduous forest were primarily controlled by the sensitivity of GPP to air temperature and the timing of leaf-out. GPP-linked controls on NEE have been observed in other aspen forests (Black et al., 2000; Barr et al., 2006; Chen et al., 2006) and changes in canopy duration (mainly through adjustment of spring leaf-out) have been shown to be the most important determinant of the interannual variability of net carbon uptake in a Canadian aspen forest (Barr et al., 2006).

Spring NEE variability was greater at the deciduous forest (an 88% increase in net carbon uptake relative to 2002) than at the evergreen forest (an 18% increase in net carbon uptake relative to 2002). Contrary to that observed at the deciduous forest, spring NEE variability at the evergreen forest reflected interannual differences in R_e. Increased net carbon uptake at the evergreen

Table 2
Seasonal summary of climate and carbon fluxes for each year of the study

Year	Air T[a] (°C)	VPD[a,b] (kPa)	PPFD[a] (mol m^{-2} day^{-1})	Soil T[c] (°C)		Soil moisture[d] (VWC)		NEE[e] (g C m^{-2})		GPP[f] (g C m^{-2})		R_e[f] (g C m^{-2})	
				Aspen	Spruce	Aspen	Spruce	Aspen	Spruce	Aspen	Spruce	Aspen	Spruce
Spring (April, May and June)													
2002	6.4	1.0	36.4	2.04	−0.21	0.22	0.39	−65	−79	−143	−179	89	116
2003	7.7	1.0	34.8	1.36	0.21	0.20	0.22	−104	−121	−156	−188	66	85
2004	9.9	1.1	33.5	3.66	1.60	0.24	0.48	−122	−93	−249	−207	143	133
Late-summer (August)													
2002	11.1	0.8	19.1	8.86	6.07	0.25	0.45	−34	−39	−98	−116	62	84
2003	12.4	1.0	25.8	8.32	5.69	0.15	0.38	−45	−28	−117	−105	76	79
2004	15.5	1.3	26.4	10.26	7.75	0.08	0.20	−15	−24	−86	−105	75	86
Growing season (April through September)[g]													
2002	8.9	0.9	29.6	5.16	2.53	0.25	0.42	−162	−152	−432	−482	285	356
2003	9.0	0.9	29.9	4.33	2.39	0.19	0.31	−200	−172	−446	−432	267	282
2004	10.8	1.0	28.8	6.08	3.82	0.18	0.41	−227	−156	−529	−474	336	353

[a] Measured above the canopy and averaged across sites.
[b] Mid-day (noon – 4 p.m.) measurements only.
[c] Measured at 10 cm depth at the deciduous (aspen) and evergreen (spruce) forests.
[d] Volumetric water content (VWC, volume of water per volume of soil) measured at 11 cm depth at the deciduous forest and 22 cm depth at the evergreen forest.
[e] Integrated gap-filled eddy covariance NEE observations (over the time period in parentheses).
[f] Integrated modeled fluxes (over the time period in parentheses).
[g] We did not consider full annual carbon budgets because of limited precision of our eddy covariance instrumentation during winter. Rather we analyzed growing season means and sums from 1 April to 30 September.

forest in 2003 (53% relative to 2002) was the result of decreased R_e that appeared to be linked with relatively low levels of soil moisture. A similar study by Arain et al. (2002) also found that warm springs increased GPP more rapidly than R_e at both aspen and black spruce forests, thereby enhancing net carbon uptake. However, evergreen forests do not appear to respond to warmer springs (by increasing spring GPP) to the extent that deciduous forests are able to in years with early leaf emergence (Arain et al., 2002; Kljun et al., 2006). The reduced sensitivity at the evergreen forest may be partially caused by soils that are somewhat more buffered from air temperature increases as compared with those at the deciduous forest (soil temperatures, Table 2). Increases in growing season length (particularly changes in the spring) have been shown to increase annual net carbon uptake at deciduous forests (Goulden et al., 1996; Black et al., 2000; Barr et al., 2006) but may have little impact (Dunn et al., 2006) or even negative consequences (Monson et al., 2005) for the carbon balance of evergreen forests.

3.2.1. Late-summer drought

Early springs were followed by warmer and drier summer conditions during the 3 years of this study. Mean August air temperature and VPD increased in each year of our study, and soil moisture levels decreased in parallel (Fig. 4 and Table 2). April–September total precipitation in our study region was 20% greater than the 1937–2005 mean during 2002, 20% less during 2003 and 30% less during 2004 based on measurements recorded at the climate monitoring station in nearby Big Delta, Alaska (WRCC, 2006). During mid-summer (June, July, and August), the precipitation anomalies were even larger: 25% greater than the climate mean in 2002, 18% less in 2003, and 47% less precipitation than the climate mean during the 2004 drought (Table 1). Furthermore, April–August 2004 monthly mean air temperatures were 1.9–4.0 °C warmer than the climate mean. Although soil moisture was consistently higher at the evergreen forest than the deciduous forest, both saw a 50–55% reduction in soil moisture in August of 2004 as compared with 2002 at both surface (2 cm) and intermediate depths (11 cm at the deciduous forest and 22 cm at the evergreen forest).

As in the previously discussed case of spring warming, drought-induced changes in GPP were larger at the deciduous forest than at the evergreen forest (Table 2). Photosynthetic uptake increased at the deciduous forest (more negative GPP values) in 2003

with warmer air temperatures (a 19% increase relative to 2002). Although air temperatures were even warmer in 2004, the severe drought during this summer caused GPP at the deciduous forest to decrease to levels below 2002 (a 12% decrease relative to 2002).

GPP at the evergreen forest showed less interannual variability and a smaller decrease during the 2004 drought (a 9% decrease in both 2003 and 2004 relative to 2002). GPP of black spruce forests may be partly buffered from drought effects because of high soil moisture conditions during normal years, resulting in little to no drought stress in drier than normal years (Kljun et al., 2006). Also, high evaporative demand is not correlated with reduced GPP of black spruce forests because of low stomatal sensitivity (i.e. stomatal conductance has been observed to remain fairly constant over a wide range of VPD's) (Goulden et al., 1997; Ewers et al., 2005). Aspen, in contrast, are more sensitive to conditions of high evaporative demand at the leaf level (Dang et al., 1997; Hogg et al., 2000), and this may cause larger reductions in GPP during drought.

The impact of drought on R_e has been shown to vary with the intensity of the drought (Reichstein et al., 2002; Barr et al., 2006; Kljun et al., 2006; Krishnan et al., 2006). In many studies of forest ecosystems, drier surface soils result in decreased R_e because of the effect on the heterotrophic microbial community (Schimel et al., 1999). Surprisingly, R_e was not depressed at either the deciduous or the evergreen forest during the 2004 summer drought (Table 2). At the deciduous forest, August R_e increased during both 2003 and 2004 (by 23% and 21%, respectively, relative to 2002). August R_e varied much less at the evergreen site (changing by −6% and 2% in 2003 and 2004, respectively, relative to 2002). The effects of increased temperature on microbial and plant respiration during the 2004 drought appeared to more than offset any limitations caused by soil moisture or the availability of recently fixed carbon substrates.

At both sites, net carbon uptake was reduced during August of 2004 compared to previous (cooler and wetter) years (by 56% and 38%, respectively, for the deciduous and evergreen sites), resulting in a positive CO_2 flux anomaly to the atmosphere. This response is consistent with past observations of prolonged drought in an aspen forest (Kljun et al., 2006; Krishnan et al., 2006). Kljun et al. (2006) also found that aspen net carbon uptake was more susceptible to drought than black spruce, due to the relatively high soil moisture conditions characteristic of black spruce forests. Differences in soil moisture availability may have played less of a role in shaping the carbon uptake responses at our sites, as compared with the leaf level VPD responses described above, because both of our forests were located on well drained soils and were not underlain by permafrost.

3.3. Net growing season

We found that total growing season (April–September) net carbon uptake increased substantially in the deciduous forest as temperatures warmed during each year of our study (by 23% and 40% in 2003 and 2004, relative to 2002). In contrast, the evergreen forest showed less variability, with increases of 13% and 3% in 2003 and 2004, respectively (Table 2). Increased spring and early summer photosynthetic uptake (more negative GPP) at the deciduous forest in 2004 (by 74%), appeared to be primarily responsible for the interannual variability in growing season NEE and was linked with an increase in LAI (Fig. 3).

A consistent pattern of interannual variability in NEE is emerging from eddy covariance measurements above boreal deciduous and evergreen forests. Long term observations of boreal aspen forests show that (1) photosynthetic uptake is largely controlled by canopy duration and LAI, and that the length of the growing season seems to have little effect on the total seasonal R_e (Barr et al., 2002, 2004, 2006), and (2) the interannual variability in annual NEE of aspen is mainly controlled by the GPP response to environmental variables while changes in R_e emissions are relatively conservative from year-to-year (Black et al., 2000; Arain et al., 2002; Griffis et al., 2003; Barr et al., 2006). Our measurements from Alaska showed net carbon uptake by aspen forests was enhanced during warmer years, even though a severe mid-summer drought occurred during the warmest year, and are consistent with Canadian forest results published by Black et al. (2000) and Barr et al. (2006). Together, these results support model predictions that suggest net carbon uptake by aspen-dominated ecosystems will increase with future climate warming (Grant et al., 2006) – assuming that pathogens and disturbance agents, including insect outbreaks and severe drought events, do not change.

In contrast to the aspen forest, there was very little variability in growing season GPP measured at our Alaskan black spruce forest from year-to-year even with considerable changes in climate (temperature and drought), consistent with findings from other black spruce forests in Canada (Goulden et al., 1997; Kljun et al., 2006). Interannual variability in NEE has been shown to be dominated by differences in R_e at black

spruce forests (Goulden et al., 1998; Arain et al., 2002; Dunn et al., 2006). Large stores of soil organic matter in mature black spruce forests are sensitive to changes in soil temperatures, active layer depth, and depth to water table (Goulden et al., 1998; Hirsch et al., 2002; Dunn et al., 2006). Dunn et al. (2006) found 50% more variability in R_e than GPP in a long term study of a black spruce forest in central Manitoba. Ecosystem models suggest that black spruce may be a weak carbon sink in cool years and a weak carbon source in warm years (Arain et al., 2002), however measurements of NEE show that the water balance of the forest is also important for protecting soil carbon from R_e loss to the atmosphere (Dunn et al., 2006).

4. Conclusions

Simultaneous eddy covariance NEE measurements of deciduous and evergreen forests in years experiencing different climate conditions showed that warm springs and summer drought resulted in greater variability in NEE and GPP at a deciduous forest than at an evergreen forest. This result implies that (1) the current variability in atmospheric CO_2 in the northern hemisphere may have a disproportionately higher contribution from deciduous forests than from evergreen conifer forests, after normalizing by surface area and (2) an increase in fire and other forms of boreal forest disturbance (e.g., Flannigan et al., 2001) that promote the growth of deciduous plant functional types may increase the magnitude of CO_2 interannual variability in the northern hemisphere.

Our results also suggest that the observed spring warming trend (Hansen et al., 2006) may enhance carbon uptake by deciduous forests but have little or no effect on growing season carbon uptake by evergreen forests. The differences in the CO_2 flux response to climate variability measured here (and reported in other studies from Canada) may help us to better understand physiological responses of deciduous and evergreen forests to climate change over the next several centuries. In this context, other stand-level processes, including disturbance events, seed dispersal, recruitment, and sapling mortality may be equally important in determining the species composition and carbon balance of boreal regions. For example, Humphreys et al. (2006) showed that differences in net carbon uptake among different aged stands in a Douglas fir chronosequence were an order of magnitude greater than the differences within a stand from year-to-year. The differences in growing season NEE between the deciduous and evergreen forests in this study were comparable to the interannual variability observed at the deciduous forest.

The carbon balance of the boreal forest is an important feedback to the global climate system and predictions of changes in carbon uptake with future climate warming critically depend on concurrent changes in the hydrological cycle (i.e. whether precipitation increases will keep pace with increased evaporative demand due to warming and increased growing season length) (McGuire et al., 2006). Spring warming is leading to increased carbon uptake by forests early in the growing season, however, careful observations of plant and soil microbial response to mid-summer drought events will be necessary to determine the annual mean response of boreal forest ecosystems to future climate change.

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