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Controlling factors on the interannual CO_2 budget at a subarctic black spruce forest in interior Alaska

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ABSTRACT

The eddy covariance method was applied to measure net ecosystem CO_2 exchange (NEE) at a subarctic black spruce forest in interior Alaska during 2003 and 2004. To clarify the budget of CO_2, we divided photosynthesis and respiration by applying the Carbon Budget Analysis Tool, in which the potential photosynthetic rate, the light use efficiency, and the suppression factors on photosynthesis were evaluated.

The potential photosynthetic rate and the light use efficiency were related with the understory leaf area index. The determined optimal temperature of photosynthesis was higher than 15 °C, which was higher than that of other boreal forests. Drought in midsummer of 2004 suppressed both photosynthesis and respiration, but the suppression was more effective in photosynthesis, resulting in a slightly decreased NEE. Cumulative respiration and photosynthesis were 2.29 and -2.50 kg CO_2 m^{-2} in 2003, and 2.37 and -2.44 kg CO_2 m^{-2} in 2004, resulting in calculated annual CO_2 sink budgets of -210 and -70 g CO_2 m^{-2} in 2003 and 2004, respectively.

1. Introduction

Investigation of carbon exchange between terrestrial ecosystems and the atmosphere is essential to understand the global carbon cycle. The boreal forest ecosystem may be a large sink of atmospheric CO_2 (Myneni et al., 2001; Schimel et al., 2001). However, the carbon budget is sensitive to change in temperature (Lindroth et al., 1998; Chen et al., 1999; Randerson et al., 1999), depth of soil thaw (Goulden et al., 1998) and other environmental factors (Frolking, 1997), which could enhance the amplitude of the annual carbon budget from year to year (Goulden et al., 1998; Chen et al., 1999). Summer warming in arctic Alaska has accelerated during the past few decades, and further warming in relation to the ecosystem shift is estimated for the subarctic (Chapin et al., 2005). To investigate the response of the terrestrial ecosystem to climate change, long-term data sets of carbon exchange between the vegetation and atmosphere are necessary, particularly for model parameterization in the northern high latitude. The eddy covariance method is a powerful tool for evaluating net ecosystem CO_2 exchange (NEE) for long-term observation (e.g. Baldocchi et al., 1996; Goulden et al., 1996). Previous long-term measurements of arctic and boreal ecosystems were mainly conducted in dense forests in Canada (Goulden et al., 1997; Jarvis et al., 1997), and in arctic tundra in Alaska (Oechel et al., 2000; Harazono et al., 2003). However, there are few long-term measurements in the boreal forest ecosystem in interior Alaska, where it is severely cold in winter and daylight persists for many hours in summer. In order to know the ecosystem response to current arctic warming and to continue to improve parameterization of model analyses, we have conducted year-round comprehensive flux observations at a black spruce forest in interior Alaska since fall 2002 (Ueyama et al., 2006).

Most of the interior region of Alaska is located on discontinuous permafrost, which could represent a unique carbon exchange in contrast to other regions. The wide annual temperature ranges of air and soil and the low precipitation could affect both photosynthesis and respiration compared to other ecosystems. Furthermore, wide range temperature and low precipitation might affect each process differently. For instance, different responses to summer drought were reported in boreal ecosystems (Arneth et al., 2002; Iwashita et al., 2005). To better understand the ecosystem responses to the current warming, it is important to evaluate the two processes separately. The Carbon Budget Analysis Tool (CBAT) is an empirical model designed to analyse photosynthesis and respiration at the stand level, using half-hourly NEE and

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environmental factors as a big-leaf approach. Previously, CBAT successfully evaluated characteristics of the two processes at various tundra ecosystems in arctic Alaska (Yoshimoto et al., 1997; Harazono et al., 1998; Mano et al., 2003). In this paper, we will examine the dominant ecological parameters controlling the responses of a black spruce forest in a subarctic continental climate, by applying CBAT to observed data at a black spruce forest in interior Alaska. We will also examine the contributions of photosynthesis and respiration to the interannual CO_2 budget.

2. Site and method

2.1. Site condition and observation

Measurements were made at a boreal forest in Fairbanks, central Alaska (64° 52′N, 147° 51′W), where the permafrost is discontinuous. The forest is dominated by black spruce (*Picea mariana*), with height up to 6.0 m, but mostly less than 1.5 m. The understory is composed of vascular plants and low shrubs. The forest floor is tussock tundra, covered by mosses and lichens. The forest around the observation tower is old growth with the mean stand age of 120 yr (Vogel et al., 2005), and no record exists of fire disturbance to the surrounding area since 1950 (Alaska Fire Service). In order to know the seasonal change of leaf area index (LAI), a plant canopy analyser (Li-Cor, LAI-2000) was applied. Thereafter, weekly observed data by the plant canopy analyser as used as LAI.

The mean monthly temperature for Fairbanks is the lowest in January at −19.3°C; the maximum is 17.4°C in July, with an annual mean of −1.4°C (Fairbanks National Weather Service, 1980–2000 monthly mean). The average annual precipitation was 270.6 mm, in which approximately 37% fell as snow, and the rest as rain in the summer months.

CO_2, H_2O, heat and momentum fluxes were measured by using the eddy covariance method (Baldocchi, 2003). The fluctuation of wind speed and temperature were measured with a three-dimensional sonic anemometer (Campbell, CSAT3). The mixing ratios of CO_2 and water vapor were measured with an open-path infrared gas analyser (Li-Cor, LI-7500). Half-hourly turbulent fluxes were calculated from the recorded data, by correcting effects of the path-length and sensor separation (Moore, 1986) and air density effect of counter flow (Webb et al., 1980). The nighttime NEE were filtered by applying the u_* threshold with 0.2 m s^{-1}, and then filled by using temperature response functions for nighttime NEE. Details of the site conditions, the measurements, and the weather during the observations are in Ueyama et al. (2006).

3. Analysis of photosynthesis by Carbon Budget Analysis Tool

The CBAT is an empirical model designed to analyse the control parameters on photosynthesis and respiration at the stand level. The parameters are empirically determined by using meteorological factors as a big leaf approach, which mainly consist of two processes, photosynthesis, P, and respiration, R_{eco}.

$$\mathrm{NEE} = P + R_{\mathrm{eco}}, \tag{1}$$

where P is defined as potential photosynthesis, P_0, and suppression effects caused by environmental factors. The potential photosynthesis is defined as a rectangular hyperbola function of PAR (Monsi and Saeki, 1953).

$$P_0 = \frac{P_{\max} b\,\mathrm{PAR}}{P_{\max} + b\,\mathrm{PAR}}, \tag{2}$$

where $P_{\max}$ and b are the hypothetical maximum of photosynthesis and the light use efficiency. The suppression effects are defined according to a simple conductance model (Jarvis, 1976), assuming that the different instances of photosynthesis on the same PAR occur under different environmental stresses.

$$P = P_0 g_{\max} f(T_a) f(\mathrm{VPD}) f(\mathrm{PAR}), \tag{3}$$

where $g_{\max}$ is the maximum normalized ecosystem conductance, PAR is photosynthetically active radiation, T_a is air temperature at 4 m, and VPD is vapour pressure deficit. f represents suppression functions, which range between 0 and 1. The response to air temperature is also described as follows (Jarvis, 1976):

$$f(T_a) = \left(\frac{T_a - T_l}{T_{\mathrm{opt}} - T_l}\right)\left[\left(\frac{T_h - T_a}{T_h - T_{\mathrm{opt}}}\right)^{(T_h - T_{\mathrm{opt}})/(T_{\mathrm{opt}} - T_l)}\right], \tag{4}$$

where T_{opt} is the optimal temperature, T_h is the maximum temperature at which $f(T_a)$ is reduced to zero, and T_l is the minimum temperature at which $f(T_a)$ is reduced to zero. The response to vapor pressure deficit was described as a simple linear function. Finally, the response to PAR is described as a rectangular hyperbola (Kosugi et al., 1995).

$$f(\mathrm{PAR}) = \frac{\mathrm{PAR}}{\mathrm{PAR} + g_{\max}/a_g}, \tag{5}$$

where a_g is the initial slope of the light-conductance curve.

The ecosystem respiration, R_{eco}, is defined by a simple exponential relationship.

$$R_{\mathrm{eco}} = R_0 \exp\left[\frac{\ln(Q_{10})}{10} T_a\right], \tag{6}$$

where R_0 is the ecosystem respiration at the reference temperature, 0°C and Q_{10} is the temperature sensitivity coefficient.

4. Results

4.1. Seasonal change of LAI

The seasonal change of LAI in 2004 is shown in Fig. 1. LAI above 1.0 m is also shown for 2004 and 2005. LAI was averaged from 80 measurement locations because of sparse black spruce structure. Observed LAI showed a clear seasonal variation, in which LAI gradually increased from 1.2 $m^2\ m^{-2}$ after spring thaw around day of year (DOY) 115 to 2.4 $m^2\ m^{-2}$ at midsummer around

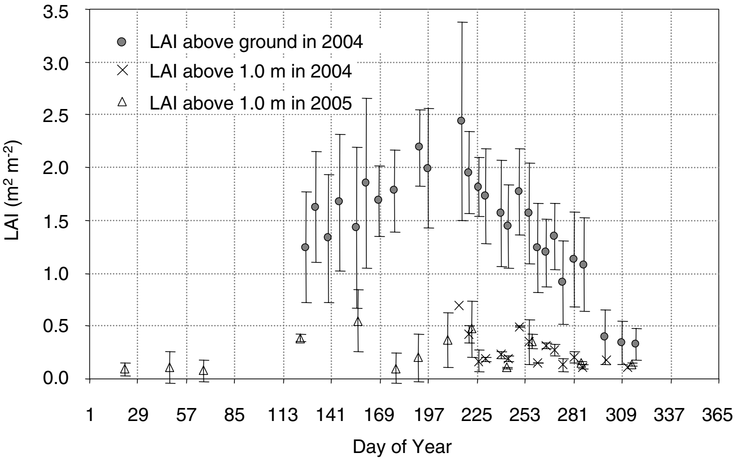

Fig. 1. Seasonal variations of LAI above ground and above 1.0 m in 2004 and 2005.

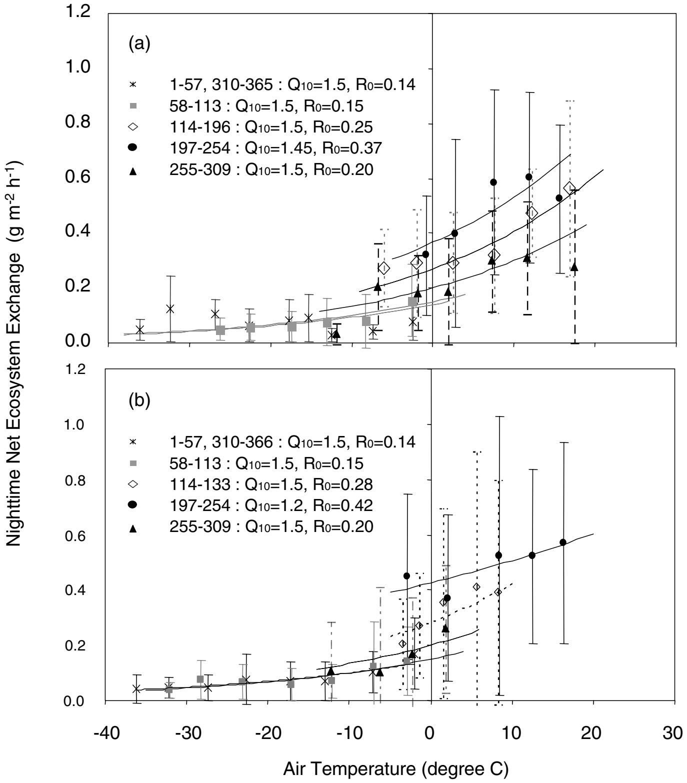

Fig. 2. Relationships between ecosystem respiration and air temperature during (a) 2003 and (b) 2004. Each data points are mean and bars are standard error.

DOY 220, and then decreased. LAI above 1.0 m, on the other hand, did not show a clear seasonality, and varied between 0.5 and 0.1 m^2 m^{-2}, suggesting that leaf area of the black spruce had little seasonality. Therefore, the seasonal variation of LAI above the ground might represent the phenology of the understory.

4.2. Ecosystem respiration

The relationship between nighttime respiration and air temperature changed when the divided periods were compared (Fig. 2). The Q_{10} value was about 1.5 throughout the year, except 1.2 during DOY 197–254 in 2004. The declined Q_{10} value was only obtained during the drought period (shown in 4–4). On the other hand, R_0 changed through the season from 0.14 to 0.42 g CO_2 m^{-2} h^{-1} in both years. The shifts in R_0 during the growing season were related to increased biomass; LAI increased from 0.5 to 2.5 m^2 m^{-2} during the growing season, which could enhance maintenance respiration. Previous studies also showed that the relationships between the ecosystem respiration and temperature changed within the growing season (Goulden et al., 1997, 1998). These changes were thought to reflect the changes in basal metabolism of above-ground spruce or moss (Skre and Oechel, 1981; Goulden et al., 1997). The R_0 shift could be caused by not only the basal metabolism but also to change of the active layer depth. A deepening active layer could increase the decomposed CO_2 emission the same as in a boreal forest (Goulden et al., 1998). The results suggested that the ecosystem respiration in subarctic forests must be estimated separately in each season, applying different relationships for several periods within a growing season.

4.3. Ecosystem photosynthesis

Since the daytime CO_2 uptake and nighttime respiration showed a clear seasonality, we divided the observation period into 13 terms for analysis, and then parameters of CBAT were determined for each term. The parameters were assumed constant within each term, because the LAI were relatively the same values within each term (Fig. 1). The half-hourly photosynthetic rate was determined from eq. (1) using R_{eco} and observed NEE. According to the conventional respiration of the eddy flux observation, downward NEE and ecosystem photosynthesis, namely CO_2 uptake by the ecosystem, was shown as negative values.

The relationships between PAR and the ecosystem photosynthesis for 13 terms were shown in Fig. 3, in which each curve showed rectangular hyperbola functions fitted to the maximum values. The photosynthesis during midwinter was almost zero and did not have significant relationships with PAR, suggesting that the black spruce stand was at dormancy under extreme cold weather and insufficient radiation. Clear relationships between PAR and photosynthesis started from late winter to early spring, DOY 58–85, when the forest floor was still covered by snow. After the spring thaw, DOY 115, the photosynthetic rate gradually increased and achieved the maximum level during DOY 198–225. During DOY 254–281, the photosynthetic rate rapidly decreased and became the same level as that during DOY 58–113. Although the stand level photosynthesis increased with PAR until the light saturation point of about 800 μmol m^{-2} s^{-1}, the photosynthesis above the point did not show a clear relationship with PAR in each term. Particularly during DOY 198–225, the photosynthetic rate was decreased at high PAR.

The potential photosynthetic rate, P_{max}, and the light use efficiency, b, showed clear seasonal variations (Fig. 4), and trends were similar between 2003 and 2004. P_{max} ranged from 0.1 to 3.8 g CO_2 m^{-2} h^{-1}, and peaked between late July and early August, which were higher in 2003. The seasonal change of b was similar to P_{max}, but the peak in 2004 was later and higher than that in 2003. The different levels of P_{max} and b were attributed to different weather conditions, such as air temperature, rainfall, and smoke cover by wildfires, in each year. These parameters also contributed to the CBAT calculation.

As temperature, vapor pressure deficit, and light intensity are known as key factors to control the photosynthesis of boreal forest ecosystems (Goulden et al., 1997; Jarvis et al., 1997; Chen et al., 1999), we examined these factors as suppression factors controlling the ecosystem photosynthesis, by applying eq. (3).

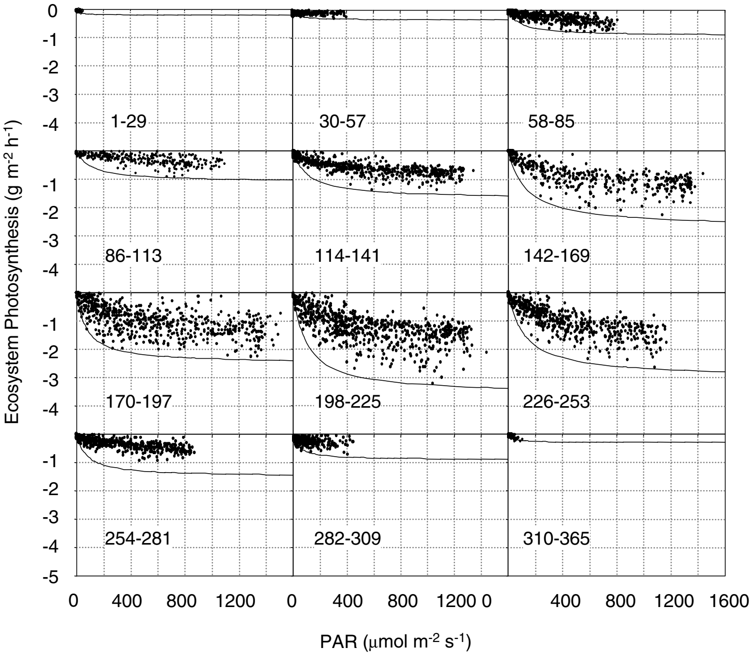

Fig. 3. Seasonal variations of relationship between ecosystem photosynthesis and PAR during 2003.

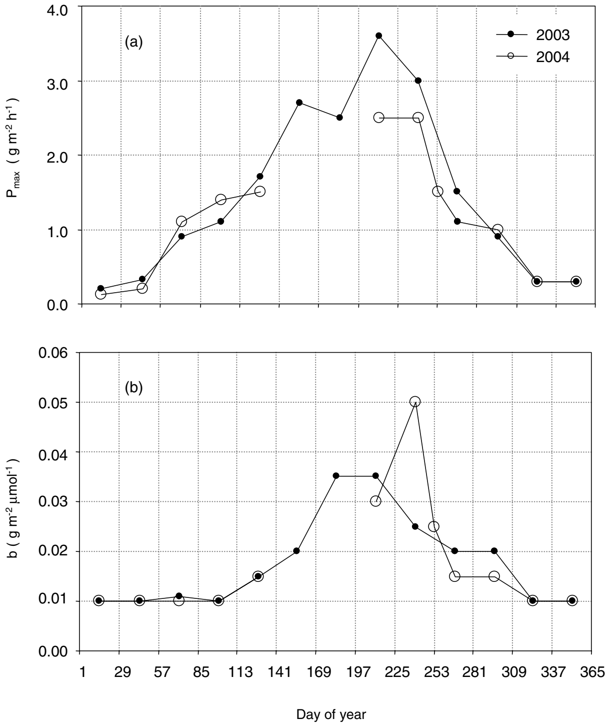

Fig. 4. Seasonal variations of (a) potential photosynthetic rate, $P_{\max}$ and (b) light use efficiency, *b*, during 2003 and 2004.

The suppression functions for air temperature, PAR and VPD are shown in Fig. 5. The suppression function theoretically takes 1.0 at its maximum, but the extent of each observed suppression was randomly affected by other suppression and also affected by other excluded parameters. Consequently, the lines in the figures were drawn to fit the observed suppression. The suppression function for VPD was negatively related with VPD during limited terms, DOY 142–197 of 2003 and DOY 201–245 of 2004. In calculation of eq. (3), consequently, we only applied the suppression of VPD for the above limited terms. The suppression effects of VPD were different in each term, in which the slopes of the linear function were −0.0072 in DOY 142–197 of 2003, −0.0063 in DOY 197–224 of 2004 and −0.0041 in DOY 225–245 of 2004. The suppression function for air temperature was examined by fitting to eq. (4). The results showed that the suppression function for temperature gradually increased with increasing temperature. An examined optimal temperature was about 22°C. During midwinter DOY 1–57 and 310–365, on the other hand, a clear relationship between air temperature and suppression function was not found. Consequently, we selected the mean value of the suppression function for temperature, 0.45. The relationship with PAR was determined within the optimal temperature, by fitting eq. (5), in which $g_{\max}$ ranged between 1.00 and 0.69 and a_g was 0.006. The derived suppression functions for environmental factors were used in CBAT to estimate photosynthesis throughout a year.

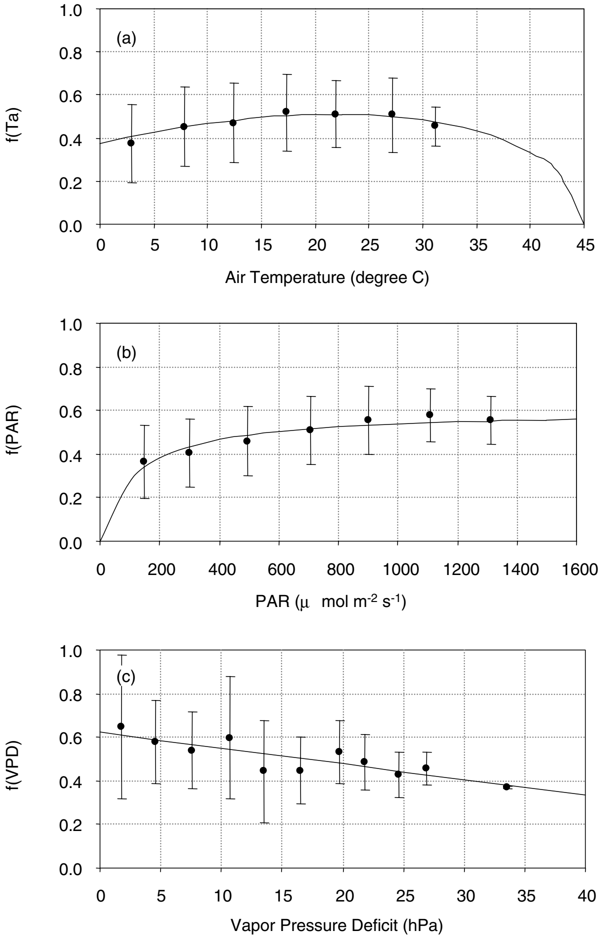

Fig. 5. Relationships between suppression function and (a) air temperature, (b) PAR and (c) vapour pressure deficit.

4.4. Meteorological inputs

The meteorology used to calculate CBAT, air temperature, VPD and PAR measured at the site in 2003 and 2004 are shown in Fig. 6 as 7-d running means. Cumulative rainfall is also shown. The snow-free period was DOY 115–290 in 2003 and DOY 115–300 in 2004. In this paper, we defined the growing season as the snow-free period. The average air temperature during the growing season in 2004 was about 2.7°C higher than that in 2003. Although rainfall in 2004 was higher than 2003 until June, a drought occurred after DOY 170 in 2004. Consequently, the rainfall during the growing season in 2004 was 140 mm, which was about half of that in 2003, 238 mm. VPD during the early growing season was high between DOY 140 and 190 in 2003 in relation to low rainfall. On the other hand, VPD was higher in the late growing season in 2004.

4.5. Comparisons of CBAT outputs and observed NEE

We calculated half-hourly photosynthesis, respiration and NEE, by applying meteorological data and parameters derived from

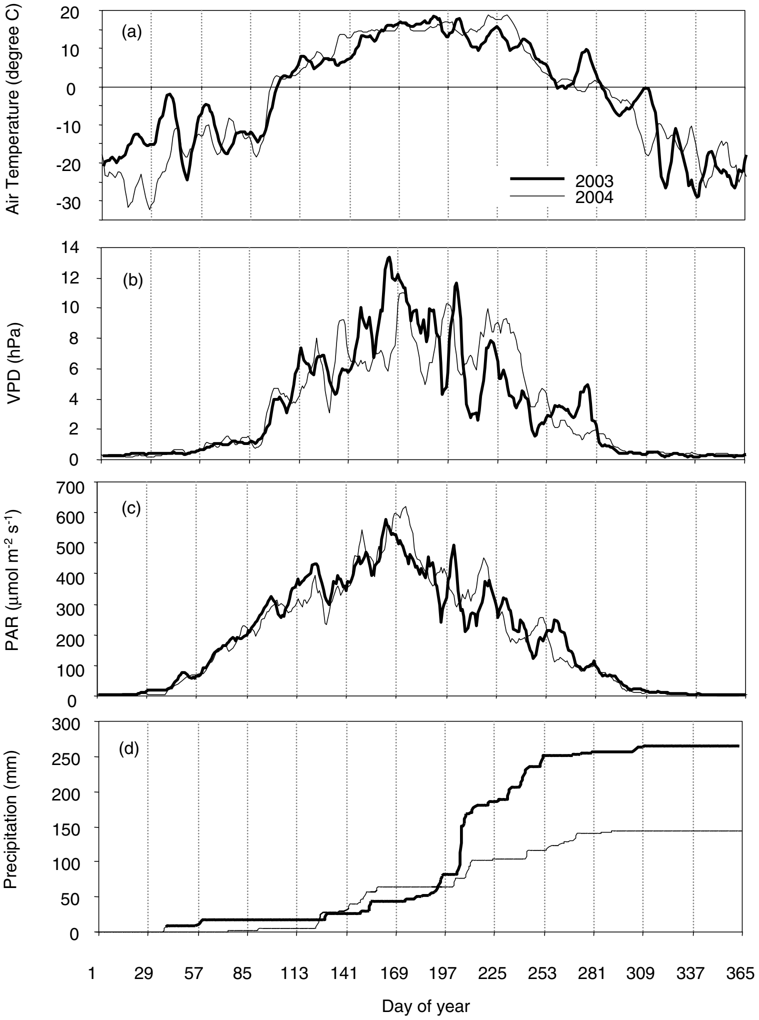

Fig. 6. Seasonal variations of (a) 7-d running mean air temperature, (b) VPD, (c) PAR and (d) cumulative rainfall in 2003 and 2004.

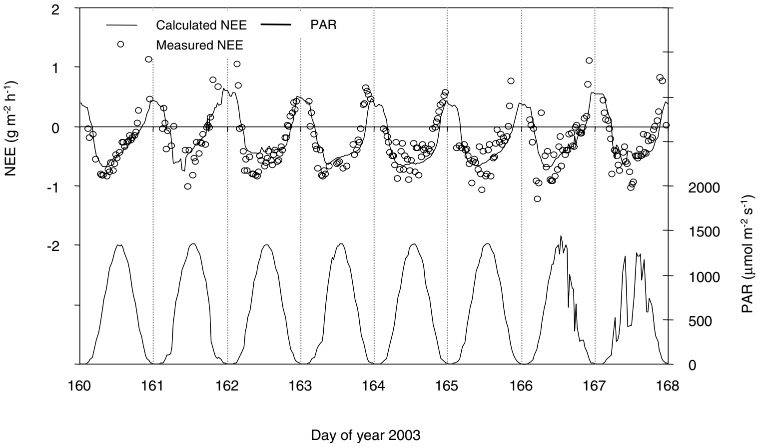

Fig. 7. Comparison diurnal variations of calculated NEE using CBAT (line) and measured NEE (circles), under variable PAR (bottom of the figure) conditions during the middle to end June 2003.

CBAT. Diurnal variations of calculated half-hourly NEE, measured NEE, and PAR between DOY 160 and 168 in 2003 were shown in Fig. 7 as an example. The relationship between observed and calculated NEE is shown in Fig. 8. For all data, the regression line underestimated the data by 30%. However, for the range between -1.0 and 0.5 g CO_2 m^{-2} s^{-1}, the underestimation was less than 7%. Since more than 90% of the half-hourly data were in this range, the model estimation seems to reflect the

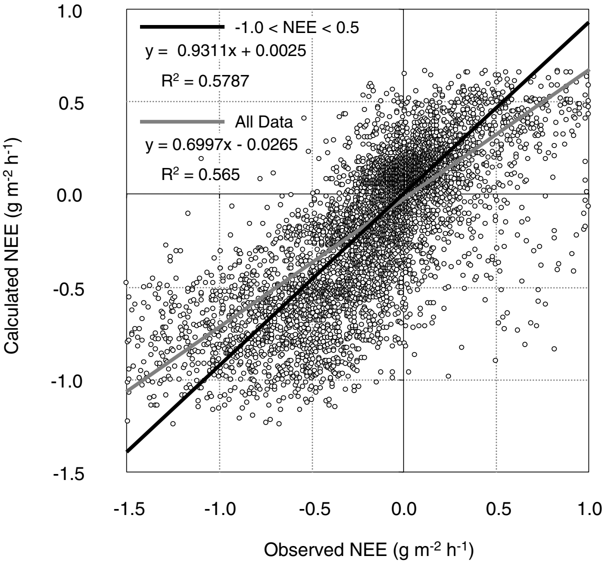

Fig. 8. Comparison of half-hourly mean of NEE between CBAT and measured.

relationship between NEE and meteorology. One reason for the poor relationship between all data was because each parameter was derived for term-averaged characteristics, which resulted in a failure to estimate peak values (Fig. 7).

The daily integrated NEE compared with the CBAT calculation and the measured values are shown in Fig. 9. Gray areas represent data gaps caused by equipment error. The calculation by CBAT could satisfactorily reproduce the observed daily NEE. The observed annual budget was -250 g CO_2 m^{-2} in 2003 and -150 g CO_2 m^{-2} in 2004, which was applied to quality control and gap filling using the mean diurnal variation method (Falge et al., 2001). However, CBAT provided annual sinks of -210 and -70 g CO_2 m^{-2} in 2003 and 2004, which were underestimates of the annual budget by about 40 g CO_2 m^{-2} in 2003 and 80 g CO_2 m^{-2} in 2004. The underestimation may be caused by the failed estimations of peak values by CBAT. Nonetheless, CBAT successfully reproduced the diurnal changes of NEE and interannual variations as well. Therefore, the calculated photosynthesis and respiration by CBAT were available to examine the interannual variation, and then the reasons for the difference in the annual CO_2 budget may be clarified.

4.6. *Interannual variation of net ecosystem exchange*

The interannual variations of a 7-d running mean of CBAT components, respiration, photosynthesis and NEE, are shown in Fig. 10, in which the ratio between photosynthesis and respiration (P/R_{eco}), were also shown. P/R_{eco} represents the relative contribution of each process to daily NEE, in which P/R_{eco} below one represents the CO_2 source and above one represents the CO_2 sink. Photosynthesis began around DOY 58, and rapidly increased to a peak, about -25 g CO_2 m^{-2} d^{-1} around DOY 210 in 2003 and about -20 g m^{-2} CO_2 d^{-1} around DOY 175 in 2004, respectively. Although maximum solar radiation occurred at solstice DOY 172, the peak of photosynthesis lagged in 2003. After the peak, photosynthesis rapidly decreased in 2003. During mid winter, ecosystem photosynthesis was almost zero. On the other hand, respiration ranged between 1.5 and 2.0 g CO_2 m^{-2} d^{-1} during midwinter. Respiration rapidly increased after around DOY 100 in relation to the rapid increase of air temperature (shown in Fig. 6). Although Fig. 10 only shows 7-d running mean values, peak levels for daily respiration occurred around 20 g CO_2 m^{-2} d^{-1} and 16 g CO_2 m^{-2} d^{-1}, at around DOY 200 in 2003 and DOY 180 in 2004 (not shown in the figure). During the decreasing trends in respiration after fall, respiration increased again due to a warming between DOY 260 and 280 in 2003 (shown in Fig. 6). Consequently, significant upward NEE was both observed and calculated (shown in Fig. 9) because photosynthesis was less sensitive to increased air temperature in this period.

P/R_{eco} showed a peak during late winter in each year, during which the value of P/R_{eco} was around 1.9 and 1.5, respectively. These peaks clearly showed the sink activity during the late winter, but the levels are relatively exaggerated because the ratio

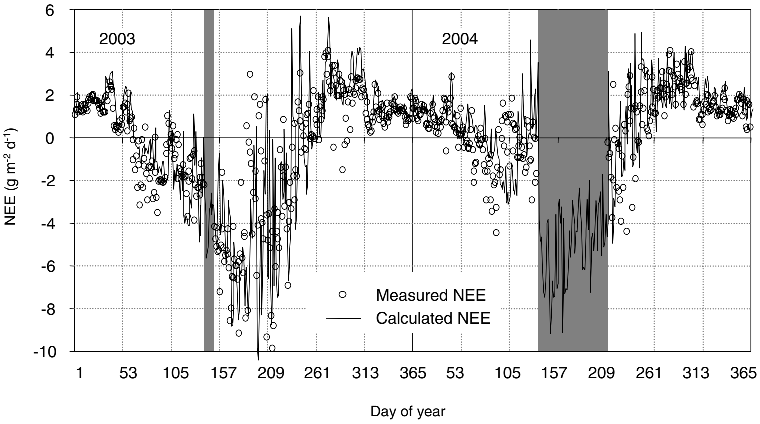

Fig. 9. Interannual variations of measured and calculated daily mean NEE. Gray area represents missing observations caused by system failure.

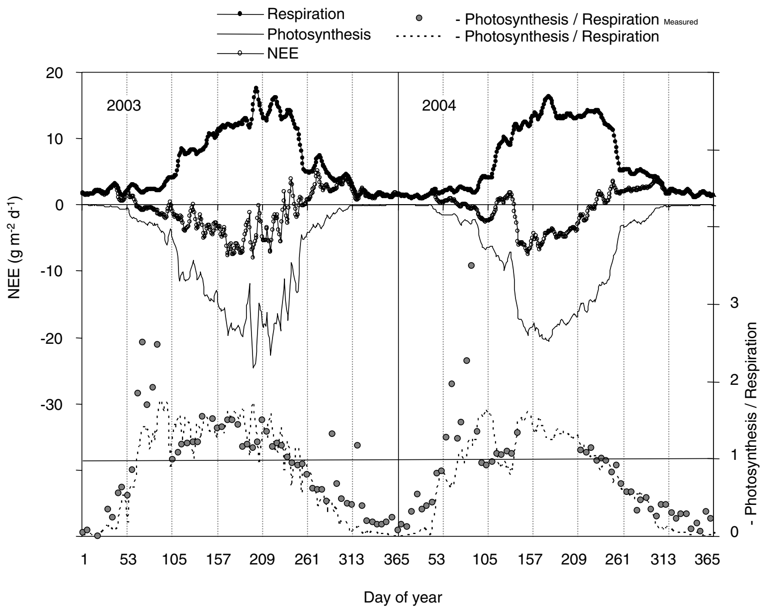

Fig. 10. Interannual variations of 7-d running mean calculated daily photosynthesis, respiration, NEE, and the calculated and observed ratio between photosynthesis and respiration.

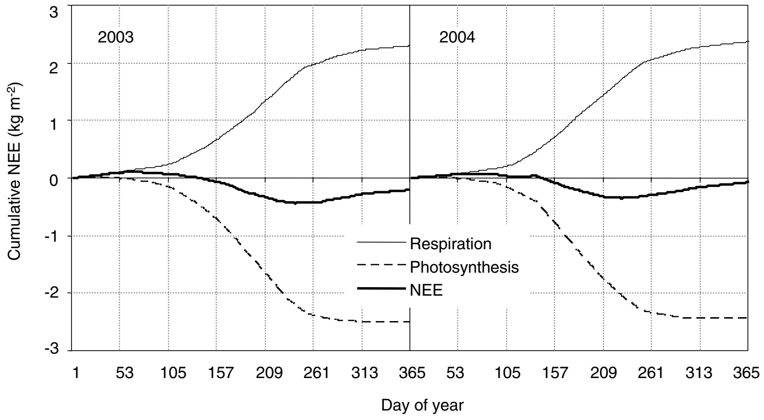

Fig. 11. The CO_2 budgets calculated using CBAT during 2003 and 2004.

was derived from fraction of small P and R_{eco} values. Between late June and early July 2003, P/R_{eco} was around 1.5, which reflected the high photosynthetic activity under the optimal air temperature and longer daylight length.

The seasonal trends of interannual CO_2 budgets and each component, respiration and photosynthesis, were shown in Fig. 11. The calculated annual CO_2 budget was the difference between the two large terms. Cumulative respiration and photosynthesis were 2.29 and -2.50 kg CO_2 m^{-2} in 2003, and 2.37 and -2.44 kg CO_2 m^{-2} in 2004, resulting in annual CO_2 sink budgets of -210 and -70 g CO_2 m^{-2} in 2003 and 2004, respectively.

5. Discussion

The obvious uptake of CO_2 occurred about 2 months before snowmelt in the subarctic black spruce forest. During this period, photosynthetic activity was obviously related to PAR (Fig. 3), while the ecosystem respiration was restricted by low air temperature and snow cover, resulting in significant sink observed as negative NEE and calculated as photosynthesis by CBAT. In this period, average temperature ranged between -5 and -20°C, although maximum temperature was around 0 °C on several days. Previously, the timing of the thaw was thought as an important factor to determine the commencement of photosynthesis (Jarvis and Linder, 2000), because the uptake of water by plants was restricted by frozen soil. Suni et al., (2003) suggested that photosynthesis commenced 1.5 months before the soil thawed, and that the water storage in tree stems could be used for transpiration until the soil thaws. The current results from field observations and CBAT analysis suggest the occurrence of photosynthesis of the black spruce forest in the subarctic before thaw. We believe that the CO_2 uptake during late winter was caused by plant photosynthesis.

The controlling factors of photosynthesis, P_{max} and b, had a positive relationship with LAI during the growing season. Since the seasonal variation of LAI at the black spruce forest was strongly affected by the understory phenology, the determined characteristics of controlling factors could be affected by the understory. LAI gradually decreased during the senescence period, while $P_{\max}$ was rapidly depleted. The rapid decline of photosynthesis could be caused by frost damage around DOY 255 in both years, when air temperature decreased to the freezing point (Fig. 6). $P_{\max}$ between DOY 197 and 253 in 2004 was lower than in 2003. One of the reasons for this decline was insufficient growth in 2004. During the early growing season of 2004, incident PAR was 11% lower than in 2003, which reduced photosynthesis to 85% compared to 2003 on CBAT calculation. The reduction of photosynthesis might have restricted the growth of vegetation. Another reason was the drought stress of the vegetation (shown below); rainfall in the growing season of 2004 was one third of that in 2003. The drought could have restricted not only the growth in earlier half of the growing season, but also $P_{\max}$ between DOY 197 and 253 in 2004.

The light use efficiency, b, during DOY 225–253 of 2004 was obviously higher than that in 2003 (Fig. 4), which could be explained by the different air temperature. Mean air temperature during the period was 2.8°C higher than that in 2003, which could have accelerated the photosynthetic enzyme. Chen et al. (1999) indicated that the photosynthesis of a boreal aspen forest was mainly limited by low b values due to low temperature at both the beginning and end of growing seasons. Lafleur et al. (2001) also showed clear seasonal variations in $P_{\max}$ and b at a boreal bog peatland, which reflected seasonal variations of LAI and temperature. Another possibility is differing light conditions in each year. In summer of 2004, severe wildfires occurred, and smoke covered most of interior Alaska resulting in continuous low solar radiation, which might increase the light use efficiency due to diffused radiation. The effect of cloudiness on light use efficiency was discussed by Fan et al. (1995), in which the conical crowns of black spruce allowed an even distribution of light over the forest during cloudy periods. In interior Alaska, the frequency of large fire years has recently increased dramatically (Kasischke et al., 2006). Smoke from these fires might increase the light use efficiency of such coniferous forests. Air temperature and wildfire smoke, therefore, could be important factors in determining the light use efficiency in interior Alaska's black spruce forest.

Determined optimal temperature of the ecosystem photosynthesis showed a higher optimal temperature than 15°C. Several studies of boreal forests showed that the optimal temperature ranged between 15 and 20°C in aspen stands (Chen et al., 1999), between 14 and 15°C in a mixed Scots pine and Norway spruce forest (Lindroth et al., 1998) and between 14 and 16°C in a black spruce forest (Goulden et al., 1997; Jarvis et al., 1997), which mainly consisted of a dense canopy with high LAI values. In contrast, our research site had a quite sparse canopy of LAI with 0.2–0.5 m^2 m^{-2} above 1.0 m. Therefore, photosynthesis of black spruce at this site could have contributed less to the total ecosystem photosynthesis, and the higher optimal temperature could reflect the characteristic of understory photosynthesis. Since most understory species were deciduous, the examined optimal temperature might adapt to summer temperature, which is comparable to that of the deciduous stands (Chen et al., 1999). The suppression by VPD was only detected for several terms, which were consistent with the low rainfall periods. The result suggested that high VPD could suppress the photosynthesis only under dry conditions. The suppression also occurred at low light intensities, which could be an adaptation to conserve water under low light (Chapin et al., 2002). The suppression function of PAR might be the correction of the simple rectangular hyperbola (eq. (2)). The suppression functions for environmental factors showed relatively scattered values (Fig. 5), which could be affected by the site heterogeneity and the contribution of the various plant responses.

The results show that the early growing season acted as an important sink period in the subarctic black spruce forest, in which the photosynthesis overwhelmed respiration. The negative NEE, the CO_2 sink, was determined as the balance between commenced photosynthesis and suppressed respiration. After snowmelt, LAI increased due to understory foliation (Fig. 1), and thus the photosynthetic activity increased rapidly (Fig. 10), while the respiration did not increase rapidly by low heterotrophic activity due to low soil and air temperature. A similar phenomenon was examined by Goulden et al. (1998). At this forest, the active layer in the early growing season was quite thin, which could not have increased the heterotrophic respiration rapidly. During the late growing season in 2003, both photosynthesis and respiration reached the maximum level, and the two processes were almost the same levels. Since the understory senescence and decreased daylight limited photosynthesis during this period, respiration was more sensitive to temperature than was photosynthesis. This result suggests that, if the recent warming trends in Alaska can increase the late growing season temperature or prolong the growing season, the CO_2 exchange during late growing season may shift to CO_2 emission.

There was a 44-d drought before DOY 210 in 2004, but we could not explain the drought effects on ecosystem CO_2 exchange because of lack of observed data during this period. However, CBAT analysis showed that the drought between DOY 210 and 253 in 2004 suppressed both photosynthesis and respiration, where the ecosystem uptake of CO_2 was slightly decreased because the suppression of photosynthesis by the drought was more effective than that of respiration. Skre and Oechel (1981) reported that photosynthesis of a moss decreased to 20% of the original level due to drought stress. A similar result was reported by Arneth et al. (2002), in which the relationship between photosynthesis and PAR were distorted by drought stress in a Russian boreal bog. A similar drought condition after the 44-d drought in 2004 also reduced the sensitivity of ecosystem respiration, Q_{10}, from 1.45 to 1.2 at the present black spruce forest, which decreased the calculated ecosystem respiration in 2004 to 90% of that in 2003, despite warmer temperatures. Although drought was generally thought to decrease the ecosystem uptake dramatically (Arneth et al., 2002; Ciais et al., 2005), the observed and calculated results suggested NEE was less sensitive to drought; the drought decreased both photosynthesis and respiration to the same degree in the present subarctic black spruce forest.

6. Conclusion

To better understand ecosystem responses to the climate, it is important to evaluate photosynthesis and respiration separately. We applied the CBAT to observed data at a black spruce forest in interior Alaska. Evaluated photosynthesis and respiration showed different seasonal trends; the commencement of the photosynthetic activity was earlier than that of respiration, resulting in a CO_2 sink being observed in the late winter and the early growing season. During the late growing season, on the other hand, photosynthesis and respiration were almost at the same levels. Drought in midsummer of 2004 suppressed both photosynthesis and respiration; during this time, NEE was slightly decreased because the suppression was more effective on photosynthesis. Recent warming prolonged the growing season in interior Alaska (Chapin et al., 2005), which could enhance the positive feedback due to both increased respiration by warmer temperature and decreased photosynthesis by subsequent drought, particularly late in the growing season. Considering the equilibrium budget of CO_2, the Alaska black spruce forests can be expected to shift to a carbon source when forced by the climate warming.

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References

Arneth, A., Kurbatova, J., Kolle, O., Shibistova, O. B., Lloyd, J. and co-authors. 2002. Comparative ecosystem-atmosphere exchange of energy and mass in a European Russian and a central Siberian bog II. Interseasonal and interannual variability of CO_2 fluxes. *Tellus* **54B**, 514–530.

Baldocchi, D. D. 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biol.* **9**, 479–492.

Baldocchi, D., Valentini, R., Running, S., Oechel, W. and Dahlman, R. 1996. Strategies for measuring and modelling carbon dioxide and water vapour fluxes over terrestrial ecosystems. *Global Change Biol.* **2**, 159–168.

Chapin, F. S., III, Matson, P. A. and Mooney, H. A. 2002. *Principles of Terrestrial Ecosystem Ecology*. Springer-Verlag Press, New York, 436 pp.

Chapin, F. S., III, Sturm, M., Serreze, M. C., McFadden, J. P., Key, J. R. and co-authors. 2005. Role of land-surface changes in arctic summer warming. *Science* **310**, 657–660.

Chen, W. J., Black, T. A., Yang, P. C., Barr, A. G., Neumann, H. H. and co-authors. 1999. Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. *Global Change Biol.* **5**, 41–53.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogée, J. and co-authors. 2005. Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* **437**, 529–533.

Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M. and co-authors. 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. *Agric. For. Meteorol.* **107**, 43–69.

Fan, S.-M. Goulden, M. L., Munger, J. W., Daube, B. C., Bakwin, P. S. and co-authors. 1995. Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: a growing season of whole-ecosystem exchange measurements by eddy correlation. *Oecologia* **102**, 443–452.

Frolking, S. 1997. Sensitivity of spruce/moss boreal forest net ecosystem productivity to seasonal anomalies in weather. *J. Geophys. Res.* **102**, 29 053–29 064.

Goulden, M. L., Munger, J. W., Fan, S.-M. and Daube, B. 1996. Measurements of carbon sequestration by long-term eddy covariance: methods and a critical evaluation of accuracy. *Global Change Biol.* **2**, 169–182.

Goulden, M. L., Daube, B. C., Fan, S.-M., Sutton, D. J., Bazzaz, A. and co-authors. 1997. Physiological responses of a black spruce forest to weather. *J. Geophys. Res.* **102**, 28 987–28 996.

Goulden, M. L., Wofsy, S. C., Harden, S. E., Trumbore, S. E., Crill, P. M. and co-authors. 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* **279**, 214–217.

Harazono, Y., Mano, M., Yoshimoto, M., Vourlitis, G. L. and Oechel, W. C. 1998. CO_2 budget of the wet sedge tundra ecosystem in Alaska, analyzed by continuously measured flux and a tundra CO_2 budget model (TCBM). *Proceedings of the Sixth Sympo. on the Joint Siberian Permafrost Studies between Japan and Russia in 1997*, pp. 159–174.

Harazono, Y., Mano, M., Miyata, A., Zulueta, R. C., Oechel, W. C. 2003. Interannual carbon uptake of a wet sedge tundra ecosystems in the arctic. *Tellus* **55B**, 215–231.

Iwashita, H., Saigusa, N., Murayama, S., McCaughery, H., Black, A. and co-authors. 2005. Effect of soil water content on carbon dioxide flux at a sparse-canopy forest in the Canadian boreal ecosystem. *J. Agric. Meteorol.* **61**, 131–141.

Jarvis, P. G. 1976. The interpretation of the vegetations in leaf water potential and stomatal conductance found in canopies in the field. *Philos. Trans. R. Soc. London. B.* **273**, 593–610.

Jarvis, P. and Linder, S. 2000. Constraints to growth of boreal forest. *Nature* **405**, 904–905.

Jarvis, P. G., Massheder, J. M., Hale, S. E., Moncrieff, J. B., Rayment, M. and co-authors. 1997. Seasonal variation of exchanges of a boreal black spruce forest. *J. Geophys. Res.* **102**, 28 953–28 966.

Kasischke, E. S., Rupp, T. S. and Verbyla, D. L. 2006. Fire trends in the Alaskan boreal forest. In: *Alaska's Changing Boreal Forest*. Oxford Press, New York, pp. 285–301.

Kosugi, Y., Kobashi, S. and Shibata, S. 1995. Modeling stomatal conductance on leaves of several temperate evergreen broad-leaved trees. *J. Jap. Soc. Reveget. Tech.* **20**, 158–167 (in Japanese with English captions and abstracts).

Lafleur, P. M., Roulet, N. T. and Admiral, S. W. 2001. Annual cycle of CO$_2$ exchange at a bog peatland. *J. Geophys. Res.* **106**, 3071–3081.

Lindroth, A., Grelle, A. and Morén, A. S. 1998. Long-term measurements of boreal forest carbon balance reveal large temperature sensitivity. *Global Change Biol.* **4**, 443–450.

Mano, M., Harazono, Y., Miyata, A., Zulueta, R. C. and Oechel, W. C. 2003. Net CO$_2$ budget and seasonal variation of CO$_2$ fluxes at a wet sedge tundra ecosystems at Barrow, Alaska during 2003 growing season. *J. Agric. Meteorol.* **59**, 141–154 (in Japanese with English captions and abstracts).

Monsi, M. and Saeki, T. 1953. Uber den lichtfaktor in den planzengesellschaften und seine bedeutung fuEr die stoffproduktion. *Jap. J. Bot.* **14**, 22–52.

Moore, C. J. 1986. Frequency response corrections for eddy correlation systems. *Boundary Layer Meteorol.* **37**, 17–35.

Myneni, R. B., Dong, J., Tucker, C. J., Kaufmann, R. K., Kauppi, P. E. and co-authors. 2001. A large carbon sink in the woody biomass of northern forests. *PANS* **98**, 14 784–14 789.

Oechel, W. C., Vourlitis, G. L., Hastings, S. J., Zulueta, R. C., Hinzman, L. and co-authors. 2000. Acclimation of ecosystem CO$_2$ exchange in the Alaskan Arctic in response to decadal climate warming. *Nature* **406**, 978–981.

Randerson, J. T., Field, C. B., Fung, I. Y. and Tans, P. P. 1999. Increases in early season ecosystem uptake explain recent changes in the seasonal cycle of atmospheric CO$_2$ at high northern latitudes. *Geophys. Res. Letter* **26**, 2765–2768.

Schimel, D. S., House, J. I., Hibbard, K. A., Bousquet, P., Ciais, P. and co-authors. 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* **414**, 169–172.

Skre, O. and Oechel, W. C. 1981. Moss functioning in different taiga ecosystems in interior Alaska. *Oecologia* **48**, 50–59.

Suni, T., Berninger, F., Vesala, T., Markkanen, T., Hari, P. and co-authors. 2003. Air temperature triggers the recovery of evergreen boreal forest photosynthesis in spring. *Global Change Biol.* **9**, 1410–1426.

Ueyama, M., Harazono, Y., Okada, R., Nojiri, A. Ohtaki, E. and co-authors. 2006. Micrometeorological measurements of methane flux at a boreal forest in central Alaska. *Mem. Natl Inst. Polar Res., Spec. Issue* **59**, 156–167.

Vogel, J. G., Valentine, D. W. and Ruess, R. W. 2005. Soil and root respiration in mature Alaskan black spruce forests that vary in soil organic matter decomposition rates. *Can. J. For. Res.* **35**, 161–174.

Webb, E. K., Pearman, G. I. and Leuning, R. 1980. Correction of flux measurements for density effects due to heat and water vapour transfer. *Quart. J. Roy. Meteorol. Soc.* **106**, 85–100.

Yoshimoto, M., Harazono, Y. and Oechel, W. C. 1997. Effects of micrometeorology on the CO$_2$ budget in mid-summer over the arctic tundra at Prudhoe Bay, Alaska. *J. Agric. Meteorol.* **53**, 1–10 (in Japanese with English captions and abstracts).