Optimization of a biochemical model with eddy covariance measurements in black spruce forests of Alaska for estimating CO₂ fertilization effects

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Abstract

Understanding how high-latitude terrestrial productivity and evapotranspiration change in association with rising atmospheric CO₂ concentration ([CO₂]), also known as ‘CO₂ fertilization’, is important for predicting future climate change. To quantify the magnitude of this fertilization effect, we have developed a big-leaf model that couples photosynthesis and stomatal conductance processes. This model was inverted by inputting eddy covariance CO₂ and H₂O fluxes from four black spruce forests in Alaska to infer spatially representative ecophysiological parameters using a global optimization technique. Inferred seasonal variations in a maximum carboxylation rate at 25°C per unit leaf area and stomatal conductance suggest greater photosynthetic capacity per unit leaf area during the mid-growing season, compared to spring and autumn. The interannual variability of parameters suggest that warm summers stimulate photosynthetic capacity and dry summers force stomatal regulation. Based on the model with optimized parameters, small but clear increases in gross primary productivity (GPP) and decreases in latent heat flux (LE) were estimated to be associated with rising [CO₂] from 2002 to 2014 ($p < 0.01$). With a 23 ppm increase in summertime (June - August) [CO₂] from 2002 to 2014, the rates of increase per unit [CO₂] were approximately 0.16 ± 0.04 % ppm⁻¹ for GPP and -0.06 ± 0.03 % ppm⁻¹ for LE from 2002 to 2014. However, considerable uncertainties (greater than 100%) were estimated in the magnitude of the fertilization effect associated with different parameterizations in the biochemical model, indicating the need for ecophysiological studies for boreal plants. A network of eddy covariance instrumentation installed across similar ecosystem types, such as the one used in this study, can be particularly useful for evaluating ecosystem-scale ecophysiological traits and their role under changing environmental conditions.

1. Introduction

Rising atmospheric CO₂ concentrations ([CO₂]) stimulate terrestrial carbon and water cycles (Keenan et al., 2013; Long et al., 2004; Koike et al., 2015; Way et al., 2015). Rising [CO₂] stimulates photosynthesis owing to increasing the carboxylation rate, because the photosynthesis of terrestrial plants at high irradiance is mostly regulated by the carboxylation rate at the current [CO₂] level (Farquhar et al., 1980; Long et al., 2004). At the same time, rising [CO₂] decreases stomatal conductance, and thus potentially decreases evapotranspiration, resulting in a potential increase in soil water (Long et al., 2004). However, the effects of rising [CO₂] on terrestrial ecosystems are variable, depending on environmental conditions, and also differ across spatial and temporal scales (Hickler et al., 2008; Long et al., 2004; Oechel et al., 1994; Shaver et al., 1992; Way et al., 2015).

Biochemical models are a useful tool for quantifying such CO₂ fertilization (Thornton et al., 2007). Many land surface models have used a biochemical model proposed by Farquhar et al. (1980), coupled with various types of stomatal conductance models (Ball et al., 1987; Damour et al., 2010; Medlyn et al., 2011). Despite similar model structures, these models predict large variability in the magnitude of the fertilization effect (de Kauwe et al., 2013; Friedlingstein et al., 2006; 2014). Part of this discrepancy is due to uncertainty in model parameters (Rogers, 2014), including a lack of understanding spatial and temporal variability in ecophysiological parameters (White et al., 2000; Feng and Dietze, 2013; Rayment et al., 2002).

The responses of the carbon and water cycles under rapid environmental change (Hinzman et al., 2005) are highly uncertain in northern high-latitude ecosystems (Chapin et al., 2005; Shaver et al., 1992). Ongoing high-latitude warming (Chapin et al., 2005; Serreze and Barry, 2011) could switch the terrestrial carbon balance to either greater sources or sinks (Euskirchen et al., 2014; Oechel et al., 2000; Ueyama et al., 2014a). Changes in energy and hydrological balances can amplify or dampen warming through processes such as changes in fire regime (Kasischke et al., 2010), methane emission (Olefeldt et al., 2013), and albedo feedbacks (Randerson et al., 2006). Because soils are nutrient-limited, the magnitude of the fertilization effect is highly uncertain in

this region (Oechel et al., 1994; Shaver et al., 1992).

Inverting ecosystem-scale ecophysiological parameters is possible by using data from a network of micrometeorological flux measurements (Groenendijk et al., 2011a, b; Ono et al., 2013; Wang et al., 2001, 2007). These eddy covariance measurements provide spatially representative, time variant, continuous carbon and water fluxes (Baldocchi et al., 2001). Inverting the eddy covariance data with various types of models reveals the seasonal and interannual variability of ecophysiological parameters (Mo et al., 2008; Owen et al., 2007; Thum et al., 2008; Wang et al., 2001, 2007; Wolf et al., 2006), spatial variations in processes related to evapotranspiration (Kasurinen et al., 2014), and ecophysiological traits under drought stress (Reichstein et al., 2003).

Black spruce forests are one of the dominant forest types in the North American boreal region, and the data from four eddy covariance sites at mature black spruce forests were used in this study. Based on these data, the objectives of this study are twofold. First, the seasonal and interannual variability of ecophysiological parameters at the ecosystem scale from black spruce forests were determined by the inversed big-leaf model with eddy covariance data. Second, the changes in gross primary productivity (GPP) and latent heat flux (LE) associated with transient rising $[\text{CO}_2]$ (CO_2 fertilization effects) were quantified with the determined parameters. This modeling approach is necessary because the period of the eddy covariance measurements is still too short to adequately provide the apparent CO_2 response for GPP or LE with a simple statistical analysis. Due to the relatively small change in CO_2 (23 ppm in 12 years) over the period of the eddy covariance measurements, the CO_2 fertilization effect in this study does not consider the changes in canopy morphology or physiology associated with CO_2 fertilization. Nonetheless, our model simulation still provides useful information as to how GPP and LE respond to $[\text{CO}_2]$ at the ecosystem scale under given morphological and physiological characteristics.

2. Materials and methods

2-1. Model

We developed a big-leaf model (inverse Big-Leaf Model for Eddy Covariance;

iBLM-EC) with coupled photosynthesis (Farquhar et al., 1980) and stomatal conductance (Ball et al., 1987) sub-models for inverting ecosystem-scale ecophysiological parameters: a maximum carboxylation rate at 25°C ($V_{C_{\max 25}}$), a maximum electron transport rate at 25°C ($J_{\max 25}$), and stomatal conductance parameters (M and B in Ball et al., 1987). Input variables are wind speed, incoming and reflected photosynthetically active photon flux density (PPFD), air temperature, relative humidity, rainfall, atmospheric pressure, $[CO_2]$, net radiation, ground heat flux, friction velocity (u_*), sensible and latent heat fluxes, GPP, and leaf area index (LAI).

Based on the biochemical model (Farquhar et al., 1980), the photosynthetic rate (A) is determined as the minimum rate of Rubisco-limited photosynthesis (A_v) and RuBP-limited photosynthesis (A_j):

$$A = \min \{A_v, A_j\} - R_l \quad (1)$$

$$A_v = V_{C_{\max}} \frac{p_i - \Gamma_*}{p_i + K_c \left(1 + p_o / K_o\right)} \quad (2)$$

$$A_j = J \frac{p_i - \Gamma_*}{4p_i + 8\Gamma_*} \quad (3)$$

where R_l is mitochondrial respiration in light, $V_{C_{\max}}$ is the maximum carboxylation rate, J is the electron transport rate, Γ_* is the CO_2 compensation point for photosynthesis in the absence of mitochondrial respiration, p_i is intercellular CO_2 partial pressure, p_o is intercellular O_2 partial pressure, and K_c and K_o are Michaelis-Menten constants. The variables $V_{C_{\max}}$, J , K_c , K_o , Γ_* , and R_l change with leaf temperature, and are often parameterized with various types of kinetic functions. We performed simulations with the biochemical model using six different parameterizations (Appendix A1, and Table A1) from de Pury and Farquhar (1997), Bernacchi et al. (2001, 2003), Collatz et al. (1991), von Caemmerer et al. (2009), Kosugi et al. (2003), and Kattge and Knorr (2007). While kinetic functions, such as the Arrhenius-type equation, were similar across the six

models with only slightly different parameterizations, a model by [Kattge and Knorr \(2007\)](#) considered the acclimation of $V_{c_{\max}}$ to growth temperature in the kinetic functions. To introduce a realistic gradual transition from one limitation to another in Eq. 1, we applied an empirical quadratic function proposed by [Collatz et al. \(1991\)](#).

Based on [Ball et al. \(1987\)](#), stomatal conductance can be modelled:

$$g_{sw} = M \frac{A}{c_s} rh_s + B \quad (4)$$

where g_{sw} is stomatal conductance to water vapor, rh_s is relative humidity at the leaf surface (Eq. A22), c_s is CO_2 concentration at the leaf surface, M is an empirical parameter for a dimensionless slope, and B is an empirical parameter for the zero intercept when net photosynthetic rate is equal or less than zero. Once g_{sw} was obtained, water vapor flux was calculated using the product of total conductance, and vapor pressure deficit (VPD) at the leaf surface.

Required inputs for determining boundary conditions, such as leaf temperature, $[\text{CO}_2]$ and water vapor concentration at the leaf surface, were estimated based on the inversion of the equations using Fick's law and the Penman-Monteith equation ([Monteith, 1965](#)), considering canopy and aerodynamic conductance ([Kosugi et al., 2005, 2013](#)) (Appendix A2). Aerodynamic conductance for scalar fluxes was estimated, considering the Stanton number using a method proposed by [Lhomme et al. \(2000\)](#). Growth temperature for assessing the acclimation of $V_{c_{\max}}$ and the maximum electron transport rate ($J_{\max}$) was calculated as a mean air temperature over the preceding thirty days ([Kattge and Knorr, 2007](#)). To solve equations 1 - 4 for photosynthesis and stomatal conductance simultaneously, we introduced an analytical solution that uses a cubic equation ([Su et al., 1997](#)).

Optimized ecosystem-scale parameter ($V_{c_{\max 25}}$) was downscaled into those for unit sun-leaf area ($v_{c_{\max 25_sun}}$) using the two-leaf sun/shade model for radiative transfer (details in Appendix A3; [de Pury and Farquhar, 1997](#)). In this study, we call values for unit ground m^{-2} as ecosystem scale, and those for unit leaf m^{-2} as leaf scale.

Downscaling was performed to eliminate both the effects of change in sun/shade fractions within the canopy and variations in LAI on the ecosystem-scale parameters. The downscaled leaf-scale parameters represent the photosynthetic capacity per unit sun-leaf and can be compared to photosynthetic capacity with different LAI. We did not downscale parameters during winter, as low LAI may introduce an erroneous estimate.

2-2. Optimization

The model parameters were globally optimized using the shuffled complex evolution method developed at the University of Arizona (SCE-UA; Duan et al., 1992, 1993, 1994). For successful global optimization, the SCE-UA introduces four concepts: a combination of random and deterministic approaches, clustering, systematic evolution, and competitive evolution. The SCE-UA was developed and used successfully to optimize hydrological models. In this study, we used the method with the settings recommended in Duan et al. (1992, 1994).

The model parameters of $V_{C_{\max 25}}$, ratio of $J_{\max 25}$ to $V_{C_{\max 25}}$ ($J_{\max 25}/V_{C_{\max 25}}$), M and B were optimized using half-hourly GPP and LE. Parameters were determined each day using an eight-day moving window for given parameter ranges with $0.1 \sim 200 \mu\text{mol m}^{-2} \text{s}^{-1}$ for $V_{C_{\max 25}}$, $1.8 \sim 2.1$ for $J_{\max 25}/V_{C_{\max 25}}$ (von Caemmerer et al., 2009; Wang et al., 2007; Wullschlegel, 1993), $0.1 \sim 100$ for M and $0 \sim 1 \text{ mmol m}^{-2} \text{s}^{-1}$ for B . Applying seasonally varying parameters with moving window allows considering changes in physiological trait, such as periodic drought stress. First, M and B were optimized by minimizing the root mean square error (RMSE) between observed and modeled LE, where observed GPP was used tentatively in Eq. 4 as an estimate of A . Coupled Eq. 4 with equations based on Fick's law, M and B were highly constrained using observed data. In the first optimization, ranges for M and B were determined based on standard deviations of ten optimized values from randomly selected initial values. Then, $V_{C_{\max 25}}$, $J_{\max 25}/V_{C_{\max 25}}$, M , and B were optimized by minimizing RMSE between observed and modeled GPP, where M and B were re-optimized for the range obtained from the first optimization for LE.

Following the above-mentioned optimization, the ratio $J_{\max 25}/V_{C_{\max 25}}$ converged

toward the lowest prescribed range (1.8) throughout all seasons for all sites. Part of this convergence could be due to equifinality under the model structure and constraints. Consequently, we used the value 1.8 rather than lowering the ratio's range, as the 1.8 value was still reasonable based on previous ecophysiological studies (von Caemmerer et al., 2009; Wang et al., 2007; Wullschleger, 1993).

Ranges of parameter uncertainty were given by ten optimized values from randomly selected initial values, as we found that the ten iterations for the optimization were enough for determining the global optima. We used optimized parameters for subsequent analyses only when parameter uncertainty was less than 10% of the absolute value.

2-3. Observations

The climate of interior Alaska is Subarctic continental (Fig. 1). Monthly mean air temperature is highest in July at $15 \pm 1^\circ\text{C}$ and lowest in January at $-25 \pm 3^\circ\text{C}$. Annual total precipitation is approximately $300 \pm 65 \text{ mm yr}^{-1}$, and approximately 20% of the precipitation falls as snow (Ueyama et al., 2014a). Vegetation in this area typically grows during the warm period from May to September, with the rest of the period characterized as a cold season with continuous snow cover (Euskirchen et al., 2014; Ueyama et al., 2014a). Interior Alaska is considered within the northern boreal forest. Based on tree-ring analysis (Ueyama et al., 2014b), the productivity of spruce trees in this region is regulated by a similar climate.

We used data from four mature black spruce (*Picea mariana*) forests in interior Alaska (Fig. 2; Table 1): the campus of University of Alaska Fairbanks (FAI; Iwata et al., 2012; Ueyama et al., 2014a), the Poker Flat Research Range (PFA; Nakai et al., 2013; Sugiura et al., 2011; Ikawa et al., 2015), the Bonanza Creek Experimental Forest (BNZ; Euskirchen et al., 2014), and a site near Delta Junction (DLS; Randerson et al., 2006; Welp et al., 2007). Forest floors were completely covered by understory species (e.g., *Betula glandulosa*, *Ledum groenlandicum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, and *Rubus chamaemorus*). Due to poorly drained lowland and permafrost conditions, *Sphagnum* moss was dominant on the forest floors at FAI, PFA, and BNZ. Feather

mosses (*Hylocomium splendens* and *Pleurozium schreberi*) and lichens were abundant over the non-permafrost soil at DLS.

Year-round micrometeorological measurements were conducted at the four sites. An open-path eddy covariance system with a sonic anemometer (CSAT3, Campbell Scientific Inc., USA) and an infrared gas analyzer (LI-7500, LI-COR, USA) was applied at FAI, BNZ, and DLS. An enclosed system with a sonic anemometer (WindMaster Pro, Gill Instruments, UK) and an infrared gas analyzer (LI-7200, LI-COR, USA) was applied at PFA. All relevant corrections for calculating fluxes were applied for each site.

We applied a consistent post-processing scheme (Ueyama et al., 2013), including quality control, u_* -filtering of nighttime data, and flux partitioning from net ecosystem exchange (NEE) into ecosystem respiration (RE) and GPP. GPP was determined as the difference between NEE and daytime RE modeled by the Q_{10} equation using nighttime data. Details about our methodology and its uncertainties have been provided in our previous studies (Ueyama et al., 2013, 2014a).

Total LAI including overstory and understory was measured using a plant canopy analyzer (LAI-2000, LI-COR, USA) every two weeks at FAI (Iwata et al., 2012; Ueyama et al., 2014). LAI at other sites was estimated from sixteen-day enhanced vegetation index (EVI) from the Moderate Resolution Imaging Spectroradiometer (MODIS) (MOD13Q1) using a relationship between measured LAI and EVI at FAI.

2-4. Data analysis

Optimization was conducted only when all input variables were qualified. We rejected data due to wet conditions during rain and within one hour after rain (Kosugi et al., 2013). We rejected data from calm conditions of $u_* < 0.1 \text{ m s}^{-1}$ or wind speed less than 0.1 m s^{-1} even in daytime, as accurate estimates of aerodynamic conductance could not been made. We did not use data from conditions of low aerodynamic conductance ($< 0.01 \text{ m s}^{-1}$) or canopy conductance ($< 0.001 \text{ m s}^{-1}$), to avoid uncertain estimates in leaf temperature. Outliers from the estimated canopy conductance and leaf temperature were filtered using a robust outlier estimator (Papale et al., 2006).

[CO₂] was input into the model after it was adjusted to the representative concentration for this region. The monthly mean of daily minimum [CO₂] at each site was adjusted to the monthly mean of [CO₂] in a well-mixed boundary layer measured at Poker Flat (interior Alaska) by the National Oceanic and Atmospheric Administration (GlobalView; http://www.esrl.noaa.gov/gmd/ccgg/globalview/co2/co2_intro.html). This adjustment was conducted because [CO₂] measured by infrared gas analyzers often suffers from offset drift. This adjustment allowed a consistent sensitivity analysis for assessing rising [CO₂] (discussed in next paragraph).

The influence of rising [CO₂] was evaluated using optimized models (hereafter, CO₂ fertilization experiment). Through the optimization, sensitive parameters for the CO₂ fertilization effect were directly determined from data; M and B defined diffusion as the supply function and $V_{c_{\max 25}}$ and $J_{\max 25}$ defined biochemical processes as the demand function for CO₂ (von Caemmerer et al., 2009), as well as aerodynamic conductance (de Kauwe et al., 2013) were directly estimated from the observed data. From 2002 to 2012, summertime (June to August) [CO₂] increased from 366 to 389 ppm according to NOAA monitoring in interior Alaska. The optimized model was run by inputting [CO₂] biased to a 2003 level. Differences in modeled GPP and LE in terms of biased and unbiased [CO₂] inputs represent direct effects of the rising [CO₂]. Note that this experiment only estimated the direct effect associated with rising [CO₂]; other indirect effects, such as structural, physiological, and morphological changes in vegetation by rising [CO₂], were not considered. To show uncertainties in the CO₂ fertilization effect, we conducted the sensitivity analysis using the optimized model with the six different parameterizations (Appendix A1). We filled short-term gaps for simulated GPP and LE using the look-up table method (Ueyama et al., 2013), so as to eliminate possible artifacts from an interannual variability in data acquisition rate.

Nitrogen use efficiency of carboxylation capacity (NUE) defined as $v_{c_{\max 25_sun}}$ divided as leaf nitrogen (N) content (Kattge et al., 2009) was estimated using a relationship at the global scale (Ryu et al., 2011). Briefly, first N content was estimated using a relationship between N and shortwave albedo (Hollinger et al., 2010; Ollinger et al., 2008), and then NUE was estimated with the $v_{c_{\max 25_sun}}$ for July. Details for the

algorithm are shown in Appendix A4.

3. Results

3-1. Evaluations of model

Our optimized model properly regenerated half-hourly and daily GPP and LE (Fig. 3, Table 2, 3). Small standard deviations in slope, RMSE, and R^2 in Tables 2 and 3 indicate that model performance using the different parameterizations was similar across the models. The slope of the linear regression showed that the optimized models slightly overestimated the peak for daily timescales. Although there were not any differences in the half-hourly performance among dry, wet, hot, and cold years, RMSE correlated with mean of sampled data ($R^2=0.51$, $p = 0.01$ for GPP and $R^2=0.85$, $p < 0.01$ for LE in FAI). This indicates that the variations in RMSE was simply associated with absolute values in GPP and LE, and the model performance was not related to the environmental conditions. RMSE in daily timescales tended to be smaller than those for half-hourly timescales, owing to reduced errors by averaging. The model was better optimized for sites with low LAI (PFA, FAI, and BNZ) compared to those with high LAI (DLS) (Table 2, 3).

3-2. Variations in parameters

The ecosystem-scale parameters of $V_{C_{\max 25}}$ showed clear seasonal variations, coinciding with those in GPP (Fig. 4, 5). Seasonal variations were associated with variations in LAI, as well as changes in photosynthetic capacity per unit sun leaf ($v_{C_{\max 25_sun}}$). The slope between $v_{C_{\max 25_sun}}$ and $V_{C_{\max 25}}$ were 0.54 in PFA, 0.58 in FAI, and 0.56 in BNZ, indicating that seasonal variations in LAI contributed approximately half of the variations in canopy-scale photosynthetic capacity. High correlations between GPP and $V_{C_{\max 25}}$ ($R^2 = 0.83$, $p < 0.01$ at FAI; $R^2 = 0.86$, $p < 0.01$ at PFA; $R^2 = 0.88$, $p < 0.01$ at BNZ; and $R^2 = 0.75$, $p < 0.01$ at BNZ) indicate that seasonal variations in GPP were associated with changes in LAI and $v_{C_{\max 25_sun}}$. In DLS, since $v_{C_{\max 25_sun}}$ in spring and autumn were unrealistically high (Fig. 5), the slope between $v_{C_{\max 25_sun}}$ to $V_{C_{\max 25}}$ was insignificant.

Ecosystem-scale parameters derived from the different parameterizations varied between spring and autumn (Fig. 5). Variations in $V_{C_{\max 25}}$ were smaller in the peak season (6% in PFA, 6% in FAI, 4% in BNZ, 9% in DLS for July) than in the early and late growing seasons (32% in PFA, 20% in FAI, 26% in BNZ, and 25% in DLS for April and October). Some parameterizations, such as Collatz et al. (1991) and Kosugi et al. (2003), showed unrealistic seasonal variations, where $V_{C_{\max 25}}$ increased during the early and late growing seasons. The parameterizations considering temperature acclimation in $V_{C_{\max 25}}$ (Kattge and Knorr, 2007) did not show unrealistically high $V_{C_{\max 25}}$.

The stomatal conductance parameters M and B were smaller in the mid-growing season (June to July) than in the early growing season except DLS (May; $p < 0.01$; Fig. 4, 5). M was related to ecosystem water use efficiency, with lower values representing higher water use efficiency due to higher stomatal regulation gaining carbon (Eq. 4). The low M associated with high $V_{C_{\max 25}}$ suggests ecosystems effectively regulated water loss during the mid-growing season. In contrast, high M and B imply that water vapor fluxes by non-stomatal regulations—such as evaporation and transpiration from mosses—contributed to canopy-scale fluxes in the early growing season. Variations in B were consistent with those in M , indicating effective stomatal control in the mid-growing season, though B in the autumn period (August-September) and the early growing season (May) was significantly greater than in the mid-growing season ($p < 0.01$).

Parameters $v_{C_{\max 25_sun}}$ and M for July (mid-growing season) showed interannual variation (Fig. 6). Interannual variations in $v_{C_{\max 25_sun}}$ and M were inconsistent across the sites. Across the measured environmental variables—including air temperature (Fig. 6c), growing degree days, daytime VPD, soil water content, and equilibrium evaporation (Fig. 6d), $v_{C_{\max 25_sun}}$ in July was positively correlated with air temperature ($R^2 = 0.48$; $p = 0.03$) and equilibrium evaporation ($R^2 = 0.52$; $p = 0.02$) at FAI. Interannual variations in M in July were positively correlated with precipitation minus equilibrium evaporation ($R^2 = 0.56$; $p = 0.01$) and negatively correlated with equilibrium evaporation ($R^2 = 0.50$; $p = 0.02$) in FAI. Fewer measurement years in PFA,

BNZ, and DLS hampered the statistical analysis.

NUE was $23.65 \pm 7.20 \mu\text{molCO}_2 \text{ gN}^{-1} \text{ s}^{-1}$ in July (Table 4). This value is similar to that for evergreen coniferous forests based on the global synthesis ($20.72 \pm 1.78 \mu\text{molCO}_2 \text{ gN}^{-1} \text{ s}^{-1}$; Kattge et al., 2009). Shortwave albedo used for estimating leaf N content was similar among sites, and thus variation in NUE for each site was determined by the variation in $v_{C_{\max 25_{\text{sun}}}}$. Interannual variations in $v_{C_{\max 25_{\text{sun}}}}$ were significantly correlated with estimated leaf nitrogen content only at BNZ ($R^2 = 0.98$; $p = 0.02$) and DLS ($R^2 = 1.00$; $p = 0.01$).

3-3. Change in fluxes due to rising CO_2 concentration

Based on the CO_2 fertilization experiment, rising $[\text{CO}_2]$ increased GPP and decreased LE (Fig. 7). The stimulations in GPP and LE were consistent at the all sites ($p < 0.01$; Fig. 7). On average, stimulation of GPP was $3.2 \pm 0.7\%$ in 2014 at FAI, $2.7 \pm 0.9\%$ in 2014 at PFA, and $3.8 \pm 0.6\%$ in 2013 at BNZ after rising $[\text{CO}_2]$ at a 2003 level (mean and standard deviation of the six different parameterizations are shown). This corresponds to a $17 \text{ g C m}^{-2} \text{ y}^{-1}$ increase in annual GPP based on the annual GPP measured at FAI ($515 \text{ g C m}^{-2} \text{ y}^{-1}$ in 2003; Ueyama et al., 2014a). LE decreased due to rising $[\text{CO}_2]$ after 2003: $-1.5 \pm 0.7\%$ in 2014 at FAI, $-1.5 \pm 0.5\%$ in 2014 at PFA, and $-0.2 \pm 0.5\%$ at 2013 of BNZ. According to a 23 ppm increase in summertime (June-August) $[\text{CO}_2]$ from 2002 to 2014, rates of the stimulation per unit $[\text{CO}_2]$ increase were approximately $0.16 \pm 0.04 \text{ \% ppm}^{-1}$ based on increases in GPP and $-0.06 \pm 0.03 \text{ \% ppm}^{-1}$ based on decreases in LE during the study period.

Considerable uncertainties were shown in the magnitude of stimulation due to the choice of parametrizations and/or formulations for physiological kinetics (Fig. 7). The increase in GPP, for example, ranged from 2.1% to 4.4% at FAI in 2014.

Increases in surface temperature associated with rising $[\text{CO}_2]$ were negligible for the stimulation of GPP over the decade. Rising $[\text{CO}_2]$ decreases stomatal conductance (Eq. 4), and then increases leaf temperature due to less latent heat dissipation. Possible effects associated with increasing leaf temperature were examined for FAI by using coupled energy budget equations with our big leaf model. According to the coupled

experiment, surface temperatures during the growing season increased only by 0.01°C with associated rising [CO₂] from 2003 to 2014. Consequently, the increase in GPP associated with the increase in leaf temperature was less than 0.1%.

4. Discussion

4-1. Ecosystem-scale parameters

The optimization technique presented here used a biochemical model and eddy covariance measurements to estimate spatially representative time-varying ecophysiological parameters. Our methodology needs only general input variables, all of which are available in micrometeorological measurements. Land surface models often use leaf-scale parameters determined by limited experiments (Rogers, 2014), resulting in biased predictions and scaling problems (Feng and Dietze, 2013; Rayment et al., 2002; Wang et al., 2007). Our technique could improve the ability to predict global terrestrial carbon and water cycles, owing to a growing number of the eddy covariance measurements (Baldocchi et al., 2011, 2014).

Optimized ecosystem-scale photosynthetic parameters showed consistent seasonal variations among black spruce forests (Fig. 4, 5). The lower photosynthetic capacities in the spring and autumn have been previously reported for the life cycle of evergreen conifers (Kosugi et al., 2013; Rayment et al., 2002) and the leaf age of deciduous leaves (Wilson et al., 2001; Muraoka et al., 2010). Since black spruce ecosystems in Alaska consist of open canopies (Nakai et al., 2013; Ueyama et al., 2014a), contributions from understory vegetation to canopy photosynthesis were large (Ikawa et al., 2015). Estimated seasonality for ecosystem-scale photosynthetic capacities could be due to a seasonal shift of species contributing to canopy photosynthesis in addition to changes in individual leaf physiology. Consequently, considerations of seasonality in parameters are important to modeling photosynthetic and evapotranspiration processes in black spruce ecosystems.

The magnitude of the estimated parameters per unit sun leaf area ($v_{C_{max25_sun}}$) were higher than those reported in previous ecophysiological studies of boreal vegetation (Fig. 5). Leaf-scale measurements have shown $v_{C_{max25_sun}}$ values of 15 ~ 25 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for

black spruce (Cai and Dang, 2002; Rayment et al., 2002), $25 \mu\text{mol m}^{-2} \text{s}^{-1}$ for white spruce (Cai and Dang, 2002), $5 \sim 14 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *Sphagnum* moss (Williams and Flanagan, 2002), and $5 \sim 7 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *Pleurozium* moss (Williams and Flanagan, 2002). Our estimates of $v_{C_{\text{max}25_{\text{sun}}}}$ are also consistent with prescribed $v_{C_{\text{max}25_{\text{sun}}}}$ in current land surface models ($43 \pm 16 \mu\text{mol m}^{-2} \text{s}^{-1}$ for boreal evergreen coniferous tree; Rogers, 2014), and inverted $v_{C_{\text{max}25_{\text{sun}}}}$ from the FLUXNET database for Canadian boreal forests ($36 \pm 16 \mu\text{mol m}^{-2} \text{s}^{-1}$; Groenendijk et al., 2011a).

The reason for the interannual variation in $v_{C_{\text{max}25_{\text{sun}}}}$ at the mid-growing season (Fig. 6) was unclear. The positive relationship between $v_{C_{\text{max}25_{\text{sun}}}}$ and air temperature in July suggests warm summers stimulated the photosynthetic capacity at FAI. This is maybe because high temperature possibly increases nitrogen availability as suggested in the Arctic tundra ecosystems (Oechel et al., 1994; Shaver et al., 1992). Due to fewer measurement years, interannual variations in $v_{C_{\text{max}25_{\text{sun}}}}$ cannot be explained at other sites. Interannual variations in physiological parameters are rarely examined in boreal forests, and thus further studies are required to clarify interannual variation. The unclear interannual variation may be due in part to the uncertainty in downscaling associated with complexity in radiative transfer in open canopies (Kobayashi et al., 2014). Incomplete downscaling may not fully separate $V_{C_{\text{max}25}}$ into $v_{C_{\text{max}25_{\text{sun}}}}$ and LAI.

Estimates for M (Fig. 5) were greater than those found in leaf-scale measurements (4-16; Ball et al., 1987; Medlyn et al., 2011). High M suggests that water use efficiency at the canopy-scale was less than at the leaf scale, due to water vapor fluxes by non-stomatal regulations. Particularly, the forest floors of the black spruce forests are wet-logged and dominated by mosses that lack stomatal regulation, while they contribute greatly to transpiration at the ecosystem scale (Ikawa et al., 2015). High M values at the canopy-scale were seen in both eddy covariance inversion at a steppe (Wolf et al., 2006) and a water-logged rice paddy (Ono et al., 2013). Part of the discrepancy between leaf-scale measurements and inversion based on eddy covariance data may be associated with methodological differences (Wolf et al., 2006).

Seasonal and interannual variations in M could be due to changes in major contributors to canopy water exchange as well as changes in ecophysiology of

vegetation. Owing to different water use characteristics, different plant functional types had different M values (Medlyn et al., 2011) and phenologies in an individual leaf (Lai et al. 2000). The positive relationship between M and precipitation minus equilibrium evaporation at FAI in July suggests greater stomatal regulation in dryer years. This sensitivity of M to water conditions might explain the inconsistency among interannual variations in M and $v_{C_{max25_sun}}$, where the latter was controlled by temperature conditions.

The range of NUE inferred from shortwave albedo and optimized $v_{C_{max25_sun}}$ was consistent with those estimated at the global scale (Kattge et al., 2009). This suggests that $v_{C_{max25_sun}}$ and thus the photosynthetic rate could be predicted for black spruce forests in Alaska, using land surface models that incorporates an albedo-N relationship (Hollinger et al., 2010; Ryu et al., 2011). In contrast, spatial variability in $v_{C_{max25_sun}}$ among the black spruce forests was not sensitive to albedo, suggesting other factors, such as canopy structure, influence the albedo-N relationship (Knyazikhin et al., 2012). Although measurements of spatially representative leaf N content are often difficult, intensive measurements of leaf N content will improve understanding of the spatio-temporal variability in the optimized $v_{C_{max25_sun}}$.

4-2. CO_2 fertilization effect

Inferring CO_2 fertilization effect using eddy covariance data could be useful, when eddy covariance data can constrain the important ecophysiological parameters related with CO_2 fertilization, such as $V_{C_{max25}}$, M and aerodynamic conductance (Groenendijk et al., 2011a, b; Kosugi et al., 2005, 2013; Ono et al., 2013; Thum et al., 2007; Wang et al., 2001, 2007). Since our study used model parameters directly inferred from observed data, the evaluated magnitude of fertilization was less uncertain than predictions from process-based models with generic parameters (Friedlingstein et al., 2006). Note that other indirect influences, such as a change in parameter associated with rising $[CO_2]$, vegetation height, and LAI, are not considered in this approach and might be important for the long-term change.

Small but certain increases in GPP and decreases in LE were estimated in association

with rising $[\text{CO}_2]$ from 2002 to 2014 ($R^2 = 0.95$, $p < 0.01$ for GPP, and $R^2 = 0.75$, $p < 0.01$ for LE; based on mean of regression slopes from changes by the six different parameterizations) (Fig. 7). These changes were smaller than those driven by climate variability: climate-induced interannual variabilities in annual GPP and LE were 15% and 9% at FAI, respectively (Ueyama et al., 2014a). Such small fertilization effects would not have been detectable without the model inversion.

The decrease in LE due to the transient increase in $[\text{CO}_2]$ was smaller than the increase in GPP. Decrease in LE was determined by decreased stomatal conductance due to increased $[\text{CO}_2]$, as well as counteractively increased stomatal conductance due to increased GPP (Eq. 4). Thus, the magnitude of the decrease in LE was smaller than the increase in GPP. Smaller magnitudes in decreased LE could be due to changes in ecophysiological parameters (Fig. 6), which might be influenced by variability in available energy (Iwata et al., 2012), VPD (Nakai et al. 2013), and soil moisture (Ohta et al., 2008). The rate of reduction in LE is particularly important in high-latitude boreal ecosystems, where the hydrological cycle is coupled with CO_2 and methane fluxes (Euskirchen et al., 2014; Olefeldt et al., 2013; Welp et al., 2007; Iwata et al., 2015), and the fire regime (Kasischke et al., 2010).

Considerable ($>100\%$) uncertainties (Fig. 7) were estimated in the magnitude of the fertilization effect associated with differently optimized $V_{c_{\max}}$ (Fig. 5) by using different parameterizations in the biochemical model. Much of the difference across parameterizations was associated with the temperature response functions of the photosynthetic parameters ($V_{c_{\max}}$, J , K_c , K_o , Γ^* , and R_l). The temperature response functions were rarely determined (Bernacchi et al., 2001, 2003), and limited information is used for land surface models as a generic parameter set (Rogers, 2014). Those parameter sets and functions generally underrepresent boreal ecosystems. However, this issue is not specific to boreal ecosystems: the magnitude of the fertilization effect is one of the major uncertainties in future projections for global carbon balance (Friedlingstein et al., 2006; 2013).

There are considerable unknowns regarding how boreal ecosystems respond to rising $[\text{CO}_2]$, due to a lack experiment such as the Free-Air CO_2 Enrichment (FACE) (Long et

al., 2004) in boreal forests (Hickler et al., 2008). Additional ecophysiological studies in boreal forests are needed. Currently, a large-scale experiment, SPRUCE (Ornes, 2013), using open-top chambers, has been conducted to assess effects of rising [CO₂] at boreal peatland near the southern border of the boreal forest. Such studies will further improve our understanding on the ecophysiology of boreal forests.

5. Conclusion

An eddy covariance network across a similar forest type (black spruce), under similar climate conditions, is useful for estimating ecophysiological parameters, because the network study provides a range of the means and variability of ecophysiological parameters across ecosystems. The optimized parameters illustrated the seasonal and interannual variations, which depended on environmental and phenological conditions. Such optimization of ecophysiological parameters can help to clarify ecosystem responses under short-term extreme weather conditions (Reichstein et al., 2003), when manual measurements are often not available, as well as general characteristics and seasonality (Groenendijk et al., 2011a, b; Kasurinen et al., 2014) and long-term responses from ecophysiological traits. The method could be a strong tool to constrain model parameters (Bonan et al., 2011, 2012), to improve regional climate model (Reyers et al. 2011), and understand ecophysiological traits and carbon balance (Owen et al., 2007) for various terrestrial ecosystems under changing environments. To better understand spatially representative parameters or for application at other sites, the source code of the model is available from the authors.

Changes in carbon and water fluxes associated with rising [CO₂] are a major concern in the current global change studies (Forkel et al., 2016; Smith et al., 2015). Optimized ecophysiological parameters could present effective modeling strategies for predicting carbon and water cycles, including for estimating the CO₂ fertilization effect. The estimated fertilization effect is small, but significant, indicating that rising [CO₂] influences the carbon and water fluxes in the high latitude forests. Quantifying such an effect is often difficult using simple statistical analyses, because small effects could be masked by interannual variability, and measurement uncertainties. Our approach is

particularly useful for quantifying the direct influence of rising [CO₂], when large scale experiments, such as FACE, are restricted due to harsh climate, remote area, or high vegetation height.

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Appendix

A1. Functions and parameters for photosynthesis model

In this section, we describe a set of kinetic functions and related parameters for the photosynthesis model that were used in our study. The parameters of the maximum carboxylation rate ($V_{C_{\max}}$), the maximum electron transport rate ($J_{\max}$), Michaelis-Menten constants (K_c , and K_o), the CO_2 compensation point for photosynthesis in the absence of mitochondrial respiration (Γ_*), and mitochondrial respiration in light (R_l) change with leaf temperature (Table A1). Basic equations for each model were originally proposed by [de Pury and Farquhar \(1997\)](#), [Bernacchi et al. \(2001, 2003\)](#), [Collatz et al. \(1991\)](#), [von Caemmerer et al. \(2009\)](#), [Kosugi et al. \(2003\)](#), and [Kattge and Knorr \(2007\)](#), but we slightly modified the models and parameterization from the original ones upon introducing our inversion scheme.

Model 1 based on de Pury and Farquhar (1997)

Temperature dependence of $V_{C_{\max}}$ ($\mu\text{mol mol}^{-1}$), K_c (Pa), K_o (Pa), and R_l ($\mu\text{mol mol}^{-1}$) are modeled by the Arrhenius function.

$$k_T = k_{25} \exp \left[E_a \frac{T_K - 298}{298 \cdot R \cdot T_K} \right] \quad (\text{A1})$$

where k_T and k_{25} are variables (e.g., $V_{C_{\max}}$, K_c , K_o , or R_l) at a given temperature and the reference temperature of 25°C , respectively. T_K is leaf temperature in Kelvin, and E_a is the activation energy (J mol^{-1}) (Table A1), and R is the universal gas constant ($8.314 \text{ J mol}^{-1} \text{ K}^{-1}$). The temperature dependence of Γ_* (Pa) and $J_{\max}$ ($\mu\text{mol mol}^{-1}$) are described as follows:

$$\Gamma_* = 3.69 + 0.188(T_K - 298) + 0.0036(T_K - 298)^2, \quad (\text{A2})$$

$$J_m = J_{\max 25} \exp \left[\frac{(T_K - 298)E_a}{RT_K \cdot 298} \right] \left[\frac{1 + \exp \left(\frac{S \cdot 298 - E_d}{R \cdot 298} \right)}{1 + \exp \left(\frac{S \cdot T_K - E_d}{R \cdot T_K} \right)} \right]. \quad (A3)$$

579

580 where $J_{\max 25}$ is the maximum electron transport rate at 25°C ($\mu\text{mol mol}^{-1}$), S is an
 581 entropy term ($\text{J K}^{-1} \text{mol}^{-1}$), and E_d is the deactivation energy (J mol^{-1}) (Table A1). The
 582 electron transport rate is described as follows:

583

$$\theta_I J^2 - (I_{le} + J_m)J + I_{le}J_m = 0 \quad (A4)$$

585

$$I_{le} = 0.5 \cdot I_1 (1 - f) \quad (A5)$$

587

588 where θ_I is the curvature of leaf response of electron transport to irradiance (0.7), J is
 589 the electron transport rate, I_{le} is PPFD effectively absorbed by PSII, I_1 is incoming PPFD,
 590 and f is the spectral correction factor (0.15).

591

592 *Model 2 based on Bernacchi et al. (2001, 2003)*

593 Temperature dependence of $V_{c\max}$ ($\mu\text{mol mol}^{-1}$), $J_{\max}$ ($\mu\text{mol mol}^{-1}$), K_c ($\mu\text{mol mol}^{-1}$),
 594 K_o ($\mu\text{mol mol}^{-1}$), Γ^* ($\mu\text{mol mol}^{-1}$), and R_l ($\mu\text{mol mol}^{-1}$) are modeled by the following
 595 function (Bernacchi et al., 2001, 2003) (Table A1).

596

$$k_T = \exp \left(c - \frac{E_a/1000}{RT_K} \right) \quad (A6)$$

598

599 where c is a scaling constant (Table A1). The electron transport rate is described as
 600 follows:

601

$$J = \frac{I_{le} + J_{\max} - \sqrt{(I_{le} + J_{\max})^2 - 4\Theta_{\text{PSII}} I_{le} J_{\max}}}{2 \cdot \Theta_{\text{PSII}}} \quad (A7)$$

$$\Theta_{\text{PSII}} = 0.76 + 0.018T - 3.7e^{-4}T^2 \quad (\text{A8})$$

$$I_{\text{le}} = 0.5 \cdot I_l \cdot a_l \cdot \Phi_{\text{PSIImax}} \quad (\text{A9})$$

$$\Phi_{\text{PSIImax}} = 0.353 + 0.022T - 3.4e^{-2}T^2 \quad (\text{A10})$$

where T is leaf temperature in degree Celsius, Θ_{PSII} is the convexity term for electron transport rates (dimensionless), a_l is the total leaf absorbance (dimensionless), and Φ_{PSIImax} is the apparent quantum yield of CO_2 assimilation (dimensionless).

Model 3 based on van Caemmerer et al. (2009)

Temperature dependence of $V_{c\text{max}}$ ($\mu\text{mol mol}^{-1}$), K_c (Pa), K_o (Pa), Γ^* (Pa), and R_l ($\mu\text{mol mol}^{-1}$) are modeled by the Arrhenius function (Eq. A1) with different parameterization (Table A1). The electron transport is based on Eq. A3 and A4, where I_{le} is defined as:

$$I_{\text{le}} = 0.5 \cdot 0.85 \cdot I_l (1 - f) \quad (\text{A11})$$

Model 4 based on Collatz et al. (2001)

Temperature dependence of $V_{c\text{max}}$ ($\mu\text{mol mol}^{-1}$), J_{max} ($\mu\text{mol mol}^{-1}$), K_c (Pa), K_o (Pa), CO_2/O_2 specificity ratio (τ) (dimensionless), and R_l ($\mu\text{mol mol}^{-1}$) are modeled by the Q_{10} function.

$$k_T = k_{25} Q_{10}^{(T-25)/10} \quad (\text{A12})$$

where Q_{10} is the relative change in the parameter for a 10°C change in temperature. In this model, the reduction of $V_{c\text{max}}$ under high temperatures is introduced in the following formula:

$$V_{c_{\max}} = V_{c_{\max 0}} \left\{ 1 + \exp \left[\frac{-220 + 703(T + 273)}{R(T + 273)} \right] \right\}^{-1} \quad (\text{A13})$$

634

635 where $V_{c_{\max 0}}$ is $V_{c_{\max}}$ calculated using Eq. A12. Temperature inhibition at high
636 temperature is also introduced for R_l .

637

$$R_l = R_{l0} \{ 1 + \exp [1.3(T - 55)] \}^{-1} \quad (\text{A14})$$

639

640 where R_{l0} is R_l calculated using Eq. A12. For calculating the electron transport rate, we
641 used the model (Eq. A4 and A5) by [de Pury and Farquhar \(1997\)](#).

642

643 *Model 5 based on Kosugi et al. (2003)*

644 Temperature dependence of $V_{c_{\max}}$ ($\mu\text{mol mol}^{-1}$) and $J_{\max}$ ($\mu\text{mol mol}^{-1}$) is calculated as
645 follow.

646

$$V_{c_{\max}} = V_{c_{\max 25}} \frac{\exp \left[\left(1 - \frac{298}{T_K} \right) \frac{E_a}{R \cdot 298} \right]}{1 + \exp \left[\frac{S \cdot T_K - E_d}{R \cdot T_K} \right]} \quad (\text{A15})$$

648

649 The temperature dependence of K_c (Pa), K_o (Pa), τ , and R_l ($\mu\text{mol mol}^{-1}$) are modeled by
650 the Arrhenius function.

651

$$k_T = k_{25} \exp \left[\left(1 - \frac{298}{T_K} \right) \frac{E_a}{R \cdot 298} \right] \quad (\text{A16})$$

653

654 For calculating the electron transport rate, we used the model (Eq. A4 and A5) by [de](#)
655 [Pury and Farquhar \(1997\)](#).

656

657 *Model 6 based on Kattge and Knorr (2007)*

Temperature dependence of $V_{c_{\max}}$ ($\mu\text{mol mol}^{-1}$) and $J_{\max}$ ($\mu\text{mol mol}^{-1}$) are calculated using Eq. A3. Temperature dependence of R_l ($\mu\text{mol mol}^{-1}$) is calculated by Eq. A6 with different parameterization (Table A1). Temperature dependence of K_c ($\mu\text{mol mol}^{-1}$), K_o ($\mu\text{mol mol}^{-1}$), and Γ^* ($\mu\text{mol mol}^{-1}$) are modeled by Eq. A1. The electron transport rate is described as follows:

$$J = \frac{I_{le} + J_{\max} - \sqrt{(I_{le} + J_{\max})^2 - 4 \cdot 0.9 \cdot I_{le} J_{\max}}}{2 \cdot 0.9} \quad (\text{A17})$$

$$I_{le} = 0.3 \cdot I_l \quad (\text{A18})$$

A2. Surface conditions at big leaf

Surface meteorological conditions near the big-leaf canopy were estimated from micrometeorological observations. Aerodynamic conductance of sensible heat (g_b ; m s^{-1}) was estimated as

$$g_b = 1 / \left(u / u_*^2 + B^{-1} / u_* \right) \quad (\text{A19})$$

where u is horizontal wind velocity (m s^{-1}), u_* is friction velocity (m s^{-1}), and B^{-1} is the parameter related to the roughness height (dimensionless). According to [Lhomme et al. \(2000\)](#), B^{-1} can be estimated using LAI (L ; $\text{m}^2 \text{m}^{-2}$) as

$$B^{-1} = a_6 L^6 + a_5 L^5 + a_4 L^4 + a_3 L^3 + a_2 L^2 + a_1 L + a_0 \quad (\text{A20})$$

where a_0 (8.9667), a_1 (16.127), a_2 (-36.403), a_3 (27.343), a_4 (-9.9967), a_5 (1.8013), a_6 (-0.128) are empirical constants. Once g_b was estimated, leaf temperature (T_{leaf} ; K) was inversely estimated using sensible heat flux (H ; W m^{-2}), and air temperature (T_{air} ; K) as

$$H = c_p \rho_{\text{air}} g_b (T_{\text{leaf}} - T_{\text{air}}) \quad (\text{A21})$$

where c_p is the specific heat ($1004 \text{ J K}^{-1} \text{ kg}^{-1}$), and ρ_{air} is air density (kg m^{-3}).

Relative humidity at the leaf surface is calculated based on [Su et al. \(1996\)](#).

$$rh_s = \frac{g_b Q_{\text{air}} + g_c Q_{\text{leaf}}}{g_b Q_{\text{leaf}} + g_c Q_{\text{leaf}}} \quad (\text{A22})$$

where Q_{air} is mixing ratio (kg kg^{-1}), Q_{leaf} is mixing ratio at leaf (kg kg^{-1}), and g_c is canopy conductance (m s^{-1}). Q_{leaf} is calculated from saturation vapor pressure at given leaf temperature. g_c is calculated based on the Penman-Monteith equation ([Monteith, 1965](#)).

$$g_c^{-1} = \left(\frac{\Delta}{\gamma} \frac{H}{\lambda E} - 1 \right) g_b^{-1} + \frac{\rho_{\text{air}} c_p D}{\gamma \lambda E} \quad (\text{A23})$$

where Δ is the rate of change of saturation vapor pressure with temperature (hPa K^{-1}), γ is the psychrometric constant (hPa K^{-1}), D is the vapor pressure deficits (hPa), and λE is latent heat flux (W m^{-2}).

A3. Downscaling ecosystem-scale parameters into leaf-scale parameters

Inverted big-leaf parameters of V_{cmax25} , J_{max25} , and B are estimated for the ecosystem scale, and are subsequently downscaled for those per unit sun-leaf area based on sun/shade fraction ([de Pury and Farquhar, 1997](#)). An ecosystem-scale parameter of X_{eco} (specifically, V_{cmax25} , J_{max25} , and B) can be divided into ecosystem-scale parameters of X_{sun} for sun leaf and X_{shade} for shade leaf.

$$\begin{aligned} X_{\text{eco}} &= X_{\text{sun}} + X_{\text{shade}} \\ &= x_{\text{sun}} L_{\text{sun}} + x_{\text{shade}} L_{\text{shade}} \end{aligned} \quad (\text{A24})$$

where x_{sun} are the parameter for unit sun-leaf area, x_{shade} are the parameter for unit shade-leaf area, L_{sun} is sunlit leaf area index, and L_{shade} is shaded leaf area index.

Assuming the proximity of vertical distribution among leaf nitrogen and irradiance, x_{sun} is written as

$$X_{\text{sun}} = X_{\text{eco}} \frac{\frac{\Omega}{k_n + k_b \Omega L_{\text{eco}}} [1 - \exp(-(k_n + k_b \Omega L_{\text{eco}}))]}{\frac{1}{k_n} [1 - \exp(-k_n)]} \quad (\text{A25}),$$

$$L_{\text{sun}} = \frac{[1 - \exp(-k_b \Omega L_{\text{eco}})]}{k_b} \quad (\text{A26}),$$

$$x_{\text{sun}} = X_{\text{sun}} / L_{\text{sun}} \quad (\text{A27})$$

where k_b is the extinction coefficient for beam PPFD, k_n is the nitrogen extinction coefficient (0.515; [de Pury and Farquhar, 1997](#)), and Ω is the clumping index (0.57 for needle-leaved forest; [He et al., 2012](#)). The extinction coefficient, k_b , is calculated as

$$k_b = G(\theta) / \cos \theta \quad (\text{A28})$$

where G is the G-function defined as the projection coefficient of foliage area on the plane perpendicular to the view direction ([Ross, 1981](#)), and θ is the solar zenith angle. We used a look-up-table among G and θ by assuming leaf angle distribution as planophile ([Pisek et al., 2013](#)).

A4. Nitrogen use efficiency

Nitrogen use efficiency of carboxylation capacity (NUE) defined as $v_{C_{\text{max}25_{\text{sun}}}}$ divided by leaf nitrogen (N) content is assessed using a known relationship at the global scale ([Ryu et al., 2011](#)). Using albedo-N relation ([Hollinger et al., 2010; Ollinger et al., 2008](#)), N concentration ($N_{\%}$; mg g^{-1}) is estimated as

$$N_{\%} = (\alpha - 0.02) / 0.067 \quad (\text{A29})$$

where α is shortwave albedo. The $N_{\%}$ is converted to leaf nitrogen content (N_c ; g m⁻²) using leaf mass per area (LMA) as

$$LMA = 10^{2.24} N_{\%}^{-0.97} \quad (A30)$$

$$N_c = 10^{-0.52} LMA^{0.38} \quad (A31).$$

Finally, NUE (μmolC gN⁻¹ s⁻¹; [Kattge et al., 2009](#)) is calculated as

$$NUE = v_{c_{\max\ 25_sun}} / N_c \quad (A32)$$

where optimized $v_{c_{\max\ 25_sun}}$ was used for calculating NUE .

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Figure and table captions:

Figure 1. Monthly mean and standard deviation of air temperature and precipitation measured at the campus of University of Alaska Fairbanks site (FAI) from 2003 to 2014. Snow precipitation in winter was measured at the Fairbanks International Airport by the National Weather Service (<https://www.ncdc.noaa.gov/>).

Figure 2. The locations of the eddy covariance sites on the digital elevation map (Global Task Team and others, 1999).

Figure 3. Comparisons of observation and optimized model for half hourly GPP (a), half hourly LE (b), daily GPP (c), and daily LE (d). Comparisons for half hourly data (a, b) were for year 2007 at FAI, and those for daily (c, d) were for years 2003-2014 at FAI, as an example.

Figure 4. Variations in daily GPP (a), LE (b), ecosystem-scale parameters $V_{c_{\max 25}}$ (c) and M (d), and LAI (e) in four black spruce ecosystems in Alaska. LAI at FAI was based on measurements with LAI-2000, whereas those at other sites were estimated using EVI from MODIS.

Figure 5. Mean seasonality of GPP, LE, ecosystem-scale parameters of $V_{c_{\max 25}}$, down-scaled parameters of $v_{c_{\max 25_sun}}$, and stomatal conductance model parameters of M , and B . Different colors for $V_{c_{\max 25}}$, and $v_{c_{\max 25_sun}}$ represent values inferred using different kinetic sub-models, with different parameters for the photosynthesis model: dPF1997 (de Pury and Farquhar, 1997), B2001 (Bernacchi et al., 2001), C1991 (Collatz et al., 1991), vC2009 (von Caemmerer et al., 2009), K2003 (Kosugi et al., 2003), and KK2007 (Kattge and Knorr, 2007).

Figure 6. Interannual variations of downscaled ecosystem-scale parameters $v_{c_{\max 25_sun}}$ (a) and M (b) for July, and mean monthly air temperature (c) and water fluxes of monthly mean precipitation and equilibrium evaporation (E_{eq}) (d) of FAI for July.

Interannual variations are shown as a coefficient of variance, calculated as anomalies divided by standard deviation. When the number of data points was less than fifteen days, the July mean was not calculated. Mean values for coefficient of variance for PFA, BNZ, and DLS were adjusted to means of particular years of FAI.

Figure 7. Changes in GPP and LE due to rising atmospheric CO₂ concentration. Fertilization effects were estimated by adjusting input CO₂ concentration level into year 2003. Analysis was done based on the coupled photosynthesis and stomatal conductance model, with optimized parameters for each site. Thin dotted lines are for DLS (2002-2004), solid lines are for FAI (2003-2014), chain lines are for BNZ (2010-2013), and dashed lines are for PFA (2011-2014). Different colors represent estimates using different sub-model and kinetic parameters in the model: dPF1997 (de Pury and Farquhar, 1997), B2001 (Bernacchi et al., 2001, 2003), C1991 (Collatz et al., 1991), vC2009 (von Caemmerer et al., 2009), K2003 (Kosugi et al., 2003), and KK2007 (Kattge and Knorr, 2007).

Table 1. Site characteristics, including location, presence of permafrost, years in the analysis, and references associated with a given site.

Table 2. Comparisons of half-hourly GPP ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and LE (W m^{-2}) between observations and models, showing slope (Model = slope $\times$ Observation), root mean square error (RMSE), determination coefficient (R^2), and sample number (n). Mean and standard deviations of statistics are for the six different kinetic functions used in the model.

Table 3. Comparisons between observations and models of daily mean GPP ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and LE (W m^{-2}) when PPFD was greater than 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, showing slope (Model = slope $\times$ Observation), root mean square error (RMSE), determination coefficient (R^2), and sample number (n). Mean and standard deviations of statistics are for the six different kinetic functions used in the model.

Table 4. Shortwave albedo, leaf nitrogen concentration ($N_{\%}$), leaf nitrogen content (N_c), optimized $v_{C_{\max 25_sun}}$ for sun leaf, and nitrogen use efficiency of carboxylation capacity (NUE) derived by division of $v_{C_{\max 25_sun}}$ by N_c for July. Means and standard deviations are shown based on data for each measurement year. $N_{\%}$ and N_c were estimated from shortwave albedo, and $v_{C_{\max 25_sun}}$ and NUE were based on optimization using a parameterization ([Kattge and Knorr, 2007](#)).

Table A1. Parameter list of the photosynthesis model: the maximum carboxylation rate ($V_{C_{\max}}$), the maximum electron transport rate ($J_{\max}$), Michaelis-Menten constants (K_c , and K_o), the CO_2 compensation point for photosynthesis in the absence of mitochondrial respiration (Γ^*), the CO_2/O_2 specificity ratio (τ) and mitochondrial respiration in light (R_l). The values at the reference temperature (k_{25}), the activation energy (E_a), the deactivation energy (E_d), temperature response coefficient (Q_{10}), an entropy term (S), and a scaling constant are shown for each model.

Table 1 Site characteristics, including location, presence of permafrost, years in the analysis, and references associated with a given site.

Site name (code)	Location	elevation	Permafrost	Stand Age	Year	References
Poker Flat Research Range (PFA)	65.12N ^o , 147.49W ^o	211	presence	67 ^{*1}	11-14	Nakai et al. (2013), Ikawa et al. (2015)
Fairbanks (FAI)	64.87N ^o , 147.86W ^o	157	presence	86 ^{*1}	03-14	Iwata et al. (2012), Ueyama et al. (2014a)
Bonanza Creek Experimental Forest (BNZ)	64.70N ^o , 148.32W ^o	120	presence	~100	10-13	Euskirchen et al. (2014)
Delta Junction (DLS)	63.92N ^o , 145.75W ^o	492	no presence	80	02-04	Randerson et al. (2006), Welp et al. (2007)

^{*1} Based on tree ring sampling at 2012 (Ueyama et al. 2014b)

Table 2. Comparisons of half-hourly GPP ($\mu\text{mol m}^{-2} \text{s}^{-1}$) and LE (W m^{-2}) between observations and models, showing slope (Model = slope $\times$ Observation), root mean square error (RMSE), determination coefficient (R^2), and sample number (n). Mean and standard deviations of statistics are for the six different kinetic functions used in the model.

GPP					LE															
slope					RMSE		R^2		slope			RMSE		R^2		n				
PFA	2011	0.98	±	0.00	1.90	±	0.14	0.63	±	0.06	0.98	±	0.02	24.94	±	0.83	0.66	±	0.02	1217
	2012	0.96	±	0.00	1.88	±	0.11	0.63	±	0.05	0.97	±	0.02	25.01	±	0.80	0.68	±	0.02	833
	2013	0.97	±	0.02	1.77	±	0.25	0.70	±	0.08	1.04	±	0.02	26.33	±	1.87	0.70	±	0.04	1008
	2014	0.98	±	0.01	1.72	±	0.07	0.76	±	0.02	1.02	±	0.02	24.43	±	0.52	0.74	±	0.01	1078
	average	0.97	±	0.01	1.82	±	0.08	0.68	±	0.03	1.00	±	0.02	25.18	±	0.63	0.69	±	0.01	
FAI	2003	0.96	±	0.01	1.75	±	0.15	0.75	±	0.04	1.01	±	0.02	26.34	±	1.04	0.72	±	0.02	1308
	2004	0.91	±	0.01	2.07	±	0.22	0.72	±	0.07	1.04	±	0.03	18.19	±	0.29	0.72	±	0.01	820
	2005	0.86	±	0.04	1.74	±	0.26	0.50	±	0.14	0.99	±	0.01	15.42	±	0.83	0.46	±	0.07	599
	2006	0.97	±	0.02	1.61	±	0.10	0.67	±	0.04	1.01	±	0.01	21.30	±	0.43	0.67	±	0.01	1438
	2007	0.97	±	0.02	2.47	±	0.46	0.79	±	0.08	1.06	±	0.02	26.43	±	1.91	0.70	±	0.04	2380
	2008	0.97	±	0.01	1.97	±	0.19	0.74	±	0.05	1.03	±	0.02	22.01	±	0.97	0.69	±	0.03	1998
	2009	0.92	±	0.03	2.93	±	0.26	0.64	±	0.06	1.04	±	0.01	24.10	±	1.09	0.65	±	0.03	2431
	2010	0.94	±	0.03	2.21	±	0.20	0.69	±	0.05	1.03	±	0.02	24.24	±	0.82	0.67	±	0.03	1688
	2011	0.96	±	0.02	2.76	±	0.34	0.71	±	0.07	1.04	±	0.02	23.58	±	1.33	0.62	±	0.04	2330
	2012	0.93	±	0.02	2.51	±	0.27	0.63	±	0.07	1.02	±	0.02	19.78	±	0.82	0.55	±	0.04	2196
	2013	0.95	±	0.02	2.80	±	0.25	0.55	±	0.08	1.02	±	0.01	27.12	±	1.04	0.45	±	0.05	1967
	2014	0.98	±	0.01	2.14	±	0.13	0.75	±	0.03	1.03	±	0.02	22.86	±	0.66	0.66	±	0.02	2478
	average	0.94	±	0.02	2.25	±	0.23	0.68	±	0.06	1.03	±	0.02	22.61	±	0.86	0.63	±	0.03	
BNZ	2010	0.96	±	0.02	3.40	±	0.40	0.65	±	0.08	1.06	±	0.03	26.73	±	0.94	0.70	±	0.02	1911
	2011	0.97	±	0.01	2.67	±	0.35	0.76	±	0.06	1.06	±	0.02	21.51	±	0.77	0.73	±	0.02	3658
	2012	0.97	±	0.01	2.85	±	0.35	0.73	±	0.06	1.06	±	0.02	22.93	±	0.90	0.75	±	0.02	3092
	2013	0.91	±	0.04	2.26	±	0.34	0.61	±	0.11	0.99	±	0.02	30.14	±	1.48	0.59	±	0.05	2741
	average	0.95	±	0.02	2.79	±	0.34	0.69	±	0.07	1.04	±	0.02	25.33	±	0.96	0.69	±	0.02	
DLS	2002	0.99	±	0.02	1.81	±	0.04	0.57	±	0.02	1.04	±	0.01	28.13	±	0.78	0.70	±	0.02	2722
	2003	0.92	±	0.03	1.71	±	0.12	0.54	±	0.06	1.00	±	0.01	22.81	±	0.82	0.58	±	0.03	3364
	2004	0.93	±	0.03	2.18	±	0.14	0.57	±	0.05	1.00	±	0.01	27.75	±	0.78	0.58	±	0.03	2118
	average	0.94	±	0.02	1.90	±	0.10	0.56	±	0.04	1.01	±	0.01	26.23	±	0.72	0.62	±	0.02	
average		0.95		2.23		0.67		1.02		24.05		0.65								
stdev		0.03		0.48		0.08		0.03		3.20		0.08								

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	GPP						LE						
	slope		RMSE		R^2		slope		RMSE		R^2		n
PFA	1.04	± 0.01	1.37	± 0.07	0.85	± 0.02	1.06	± 0.02	17.37	± 0.39	0.78	± 0.02	631
FAI	1.03	± 0.01	2.07	± 0.16	0.79	± 0.03	1.09	± 0.03	19.94	± 0.66	0.70	± 0.04	1771
BNZ	1.05	± 0.01	1.69	± 0.14	0.89	± 0.02	1.15	± 0.04	23.98	± 0.74	0.70	± 0.04	700
DLS	1.07	± 0.02	1.39	± 0.05	0.68	± 0.02	1.19	± 0.02	26.82	± 0.67	0.55	± 0.04	481

Table 4. Shortwave albedo, leaf nitrogen concentration ($N_{\%}$), leaf nitrogen content (N_c), optimized $vc_{\max25_sun}$ for sun leaf, and nitrogen use efficiency of carboxylation capacity (NUE) derived by division of $vc_{\max25_sun}$ by N_c for July. Means and standard deviations are shown based on data for each measurement year. $N_{\%}$ and N_c were estimated from shortwave albedo, and $vc_{\max25_sun}$ and NUE were based on optimization using the parameterization (Kattge and Knorr, 2007).

	albedo	$N_{\%}$		N_c		$vc_{\max25_sun}$		NUE		
	--	mg g ⁻¹		g m ⁻²		μmol m ⁻² s ⁻¹		umolCO ₂ gN ⁻¹ s ⁻¹		
PFA	0.16 ±	0.01	2.07 ±	0.18	1.64 ±	0.09	32.12 ±	12.33	19.60 ±	6.47
FAI	0.12 ±	0.01	1.51 ±	0.12	1.84 ±	0.06	48.84 ±	12.83	26.60 ±	7.13
BNZ	0.10 ±	0.01	1.26 ±	0.15	1.97 ±	0.07	53.86 ±	13.27	27.28 ±	7.11
DLS	0.12 ±	0.01	1.44 ±	0.17	1.89 ±	0.08	27.02 ±	12.83	14.36 ±	6.78
average	0.12 ±	0.02	1.56 ±	0.29	1.84 ±	0.12	43.49 ±	14.13	23.65 ±	7.20

Table A1 Parameter list of the photosynthesis model: the maximum carboxylation rate ($V_{c\max}$), the maximum electron transport rate ($J_{\max}$), Michaelis-Menten constants (K_c and K_o), the CO_2 compensation point for photosynthesis in the absence of mitochondrial respiration (Γ^*), the CO_2/O_2 specificity ratio (τ) and mitochondrial respiration in light (R_1). The values at the reference temperature (k_{25}), the activation energy (E_a), the deactivation energy (E_d), temperature response coefficient (Q_{10}), an entropy term (S), and a scaling constant are shown for each model.

Parameter			de Pury and Farquhar (1997)	Bernacchi et al. (2001, 2003)	von Caemmerer et al. (2009)	Collatz et al. (1991)	Kosugi et al. (2003)	Kattge and Knorr (2007)
K_c	k_{25}	Pa	40.4	--	26	30	27.5	
		$\mu\text{mol mol}^{-1}$						404.9
	E_a	J mol^{-1}	59400	79430	59360	--	80500	79430
	Q_{10}	dimensionless	--	--	--	2.1	--	--
K_o	c	dimensionless	--	38.05	--	--	--	--
	k_{25}	Pa	24800	--	17900	30000	42000	
		mol mol^{-1}						278.4
	E_a	J mol^{-1}	36000	36380	35940	--	14500	36380
$v_{\text{cmax}25}$	Q_{10}	dimensionless	--	--	--	1.2	--	--
	c	dimensionless	--	20.3	--	--	--	--
	k_{25}	$\mu\text{mol m}^{-2} \text{s}^{-1}$	optimize	optimize	optimize	optimize	optimize	optimize
	E_a	J mol^{-1}	64800	65330	58520	--	67600	71513
$j_{\text{cmax}25}$	E_d	J mol^{-1}	--	--	--	--	204600	200000
	S	$\text{J K}^{-1} \text{mol}^{-1}$	--	--	--	--	650	$668.39 - 1.07 \times T_g^{*a}$
	Q_{10}	dimensionless	--	--	--	2.4	--	--
	c	dimensionless	--	26.35	--	--	--	--
$j_{\text{cmax}25}$	k_{25}	$\mu\text{mol mol}^{-1}$	optimize	optimize	optimize	optimize	optimize	optimize
	E_a	J mol^{-1}	37000	43540	37000	--	67600	49884
	E_d	J mol^{-1}	220000	--	--	--	--	200000
	S	$\text{J K}^{-1} \text{mol}^{-1}$	710	--	--	--	--	$659.70 - 0.75 \times T_g^{*a}$
R_1	Q_{10}	dimensionless	--	--	--	2.4	--	--
	c	dimensionless	--	17.57	--	--	--	--
	k_{25}	$\mu\text{mol mol}^{-1}$	$0.0089 \times v_{\text{cmax}25}$	$0.0089 \times v_{\text{cmax}25}$	$0.0089 \times v_{\text{cmax}25}$	$0.0089 \times v_{\text{cmax}25}$	$0.0089 \times v_{\text{cmax}25}$	$0.01 \times v_{\text{cmax}25}$
	E_a	J mol^{-1}	66400	46390	66400	--	66405	46390
Γ^*	Q_{10}	dimensionless	--	--	--	2	--	--
	c	dimensionless	--	18.72	--	--	--	18.72
	k_{25}	Pa	3.69	--	3.86	--	--	
		$\mu\text{mol mol}^{-1}$						42.75
τ	E_a	J mol^{-1}	29000	37830	23400	--	--	37830
	Q_{10}	dimensionless	--	--	--	--	--	--
	c	dimensionless	--	19.02	--	--	--	--
	k_{25}	dimensionless	--	--	--	2600	2321	--
τ	E_a	J mol^{-1}	--	--	--	--	-29000	--
	Q_{10}	dimensionless	--	--	--	0.57	--	--

^a T_g is growth temperature defined as a mean air temperature over the preceding thirty days.

Figures
Figure 1

Fig. 1 Monthly mean and standard deviation of air temperature and precipitation measured at the campus of University of Alaska Fairbanks site (FAI) in Alaska from 2003 to 2014. Snow precipitation in winter was measured at the Fairbanks International Airport by the National Weather Service (<https://www.ncdc.noaa.gov/>).

Figure 2

Fig. 2 The locations of the eddy covariance sites on the digital elevation map (Global Task Team and others, 1999).

Figure 3

Fig. 3. Comparisons of observation and optimized model for half hourly GPP (a), half hourly LE (b), daily GPP (c), and daily LE (d). Comparisons for half hourly data (a, b) were for year 2007 at FAI, and those for daily (c, d) were for years 2003-2014 at FAI, as an example.

Figure 4

Fig. 4. Variations in daily GPP (a), LE (b), ecosystem-scale parameters $V_{c_{\text{max}25}}$ (c) and M (d), and LAI (e) in four black spruce ecosystems in Alaska. LAI at FAI was based on measurements with LAI-2000, whereas those at other sites were estimated using EVI from MODIS.

Figure 5

Fig. 5. Mean seasonality of GPP, LE, ecosystem-scale parameters of $V_{c_{\max 25}}$, down-scaled parameters of $v_{c_{\max 25_sun}}$, and stomatal conductance model parameters of M , and B . Different colors for $V_{c_{\max 25}}$, and $v_{c_{\max 25_sun}}$ represent values inferred using different kinetic sub-models, with different parameters for the photosynthesis model: dPF1997 (de Pury and Farquhar, 1997), B2001 (Bernacchi et al., 2001), C1991 (Collatz et al., 1991), vC2009 (von Caemmerer et al., 2009), K2003 (Kosugi et al., 2003), and KK2007 (Kattge and Knorr, 2007).

Figure 6

Fig. 6. Interannual variations of downscaled ecosystem-scale parameters $v_{C_{max25_sun}}$ (a) and M (b) for July, and mean monthly air temperature (c) and water fluxes of monthly mean precipitation and equilibrium evaporation (E_{eq}) (d) of FAI for July. Interannual variations are shown as a coefficient of variance, calculated as anomalies divided by standard deviation. When the number of data points was less than fifteen days, the July mean was not calculated. Mean values for coefficient of variance for PFA, BNZ, and DLS were adjusted to means of particular years of FAI.

Figure 7

Fig. 7. Changes in GPP and LE due to rising atmospheric CO₂ concentration. Fertilization effects were estimated by adjusting input CO₂ concentration level into year 2003. Analysis was done based on the coupled photosynthesis and stomatal conductance model, with optimized parameters for each site. Thin dotted lines are for DLS (2002-2004), solid lines are for FAI (2003-2014), chain lines are for BNZ (2010-2013), and dashed lines are for PFA (2011-2014). Different colors represent estimates using different sub-model and kinetic parameters in the model: dPF1997 (de Pury and Farquhar, 1997), B2001 (Bernacchi et al., 2001, 2003), C1991 (Collatz et al., 1991), vC2009 (von Caemmerer et al., 2009), K2003 (Kosugi et al., 2003), and KK2007 (Kattge and Knorr, 2007).