Leaf- and ecosystem-scale photosynthetic parameters for the overstory and understory of boreal forests in interior Alaska

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Abstract

Photosynthetic parameters are key for predicting the carbon cycle and fluxes in terrestrial ecosystems. In northern high-latitude regions where cold temperatures limit available nitrogen for plants, the photosynthetic parameters are tightly linked with the nitrogen content. Here, we present the leaf- and ecosystem-scale photosynthetic parameters, the maximum carboxylation rate ($v_{\text{Cmax}}$), based on leaf chamber measurements and eddy covariance data from two mature black spruce forests and one young aspen-birch forest in interior Alaska. The leaf carbon to nitrogen ratio (C:N ratio) explained most of the variations in $v_{\text{Cmax}}$ across the five vascular plants (Picea mariana, Betula glandulosa, Ledum groenlandicum, Betula papyrifera, and Populus tremuloides) ($R^2 = 0.68$; $p < 0.01$), including the overstory and understory, from the three forests. Each plant had a small within-species variability of $v_{\text{Cmax}}$ and leaf C:N, suggesting that plants have a specific potential for available N in photosynthesis. This result indicates that the canopy structure and community composition are presumably important factors for modeling the canopy photosynthesis across boreal forests in interior Alaska. The ecosystem-scale $v_{\text{Cmax}}$ determined from the eddy covariance data further supported this hypothesis.

Key words: Alaska, Boreal forest, Ecophysiology, Leaf C:N ratio, Photosynthesis

1. Introduction

Coupling carbon and nitrogen cycles is important for predicting greenhouse gas budgets of high-latitude ecosystems (Euskirchen et al., 2010) where a substantial warming trend has been observed (Chapin et al., 2005). In high-latitude ecosystems, cold temperatures limit decomposition and the available nitrogen (Euskirchen et al., 2010). Warming thus increases microbial activity and available nitrogen, potentially inducing the stimulation of photosynthetic capacities (Euskirchen et al., 2010; Ueyama et al., 2009). These processes, increases in decomposition and photosynthesis, could change the carbon budget in high-latitude ecosystems (Clein et al., 2002; Euskirchen et al., 2010).

Understanding the photosynthetic parameters of high-latitude ecosystems is important for predicting the high-latitude carbon cycle (Clein et al., 2002). Photosynthetic parameters in the North American boreal forest were reported mostly at its southern edge in Canada (e.g., Dang et al., 1997, 1998), but are rarely reported for its northern edge in interior Alaska. Black spruce (Picea mariana) is the major overstory species of the North American boreal forest (Girardin et al., 2016). In addition to the overstory, understory and pioneer species after forest fires are also important components of North American boreal forests (Ikawa et al., 2015; Welp et al., 2007).

The maximum carboxylation rate, an index of photosynthetic capacity under light saturation under current atmospheric CO$_2$ concentration (Farquhar et al., 1980), is a key parameter for predicting the carbon cycle in terrestrial ecosystems (Bonan et al., 2011). Variations in the carboxylation rate within a forest (Dang et al., 1997) and between forests (Bonan et al., 2012) characterize forest productivities, and are thus necessary information for ecosystem modeling (Bonan et al., 2011, 2012). As the maximum carboxylation rate is generally related to leaf nitrogen content (Kattge et al., 2009), this parameter links the carbon and nitrogen cycles (Clein et al., 2002).

In this study, we evaluated the photosynthetic parameters for overstory and understory plants of two black spruce and one young aspen-birch forests in interior Alaska, based on leaf chamber measurements for the leaf scale and an inversion of a canopy photosynthesis model using eddy covariance fluxes (Ueyama et al., 2016) for the ecosystem scale. We show a single relationship between the maximum carboxylation rates and the leaf carbon to nitrogen ratios (C:N ratio) within and between the forests, and discuss the linkage of the leaf- and ecosystem-scale photosynthetic parameters.
2. Measurements

2.1 Study sites

The measurements were conducted in two mature black spruce (Picea mariana) forests, and in one aspen-birch forest 12-years after a forest fire in 2004 in interior Alaska. The three sites experienced a similar boreal climate. One mature forest was located on the campus of the University of Alaska Fairbanks (FAI, 64°52'N, 147°51'W, elevation 155 m; Iwata et al., 2012; Ueyama et al., 2014a) and the other mature forest was located near Delta Junction (DLS, 63°54'N, 145°40'W, elevation 492 m; Randerson et al., 2006; Welp et al., 2007). The aspen-birch forest was located in the Poker Flat Research Range (PFF, 65°08'N, 147°26'W, elevation 491 m; Iwata et al., 2011).

The dominant overstory of the FAI and DLS forests was black spruce; FAI consisted of an open canopy on permafrost, whereas DLS consisted of a closed canopy on a non-permafrost soil. The forest floor at FAI was completely covered by Sphagnum and feather mosses and understory shrubs (e.g., Betula glandulosa, Ledum groenlandicum, Vaccinium uliginosum, Vaccinium vitis-idaea, Larix laricina, and Rubus chamaemorus). The forest floor at DLS was covered by feather mosses (Hylocomium splendens, and Pleurozium schreberi), lichens (Cladonia spp., and Stereocaulon spp.), and understory species (e.g., Ledum palustre, Vaccinium uliginosum, and Vaccinium vitis-idaea). The ages of black spruce trees were 36 to 119 years (mean of 86 years) for FAI, and 74 to 132 years (mean of 103 years) for DLS in 2012 (Ueyama et al., 2014b). The approximate mean canopy heights were 3 m for FAI, and 4 m for DLS.

The aspen-birch forest regrew at a fire scar burned in 2004 (PFF; Iwata et al., 2011). The overstory of PFF was paper birch (Betula papyrifera) and trembling aspen (Populus tremuloides), and understory vegetation (e.g., Picea mariana, Vaccinium uliginosum, Salix spp., Betula glandulosa, Carex lasiocarpa, and Polytrichum commune) was abundant in 2016. The mean and standard deviation of tree heights were 2.9 ± 0.8 m for Betula papyrifera (n = 75), 1.5 ± 0.8 m for Populus tremuloides (n = 59), and 0.24 ± 0.19 m for Picea mariana (n = 152) in August 2016.

2.2 Leaf chamber system

We developed an open chamber system for measuring the photosynthetic and transpiration rates. The branch chamber was made by a 1.5-liter transparent plastic cylindrical container (B-2265, Iwasaki Industry Inc., Japan). Air was sent to the chamber using a pump (MV-10, Enomoto Micro Pump Manufacturing Co., Japan) with a 62-liter buffer. The flow rate was recorded using a mass flow sensor (Model 3810 S, Kofloc, Japan), and ranged between 1.9 and 2.3 liters minute⁻¹. Air within the chamber was mixed with two fans for eliminating the leaf boundary resistance. CO₂ concentrations inside and outside the chamber were measured using an infrared gas analyzer (GMP343, Vaisala, Finland). To measure CO₂ concentrations, flow lines were switched using solenoid valves (USG-6-2-E, CKD, Japan). To remove dust, an air filter (RAWP 1.2 μm, Merek Millipore Ltd., USA) was placed just before the gas analyzer. The air temperature and relative humidity were measured inside and outside the chamber using temperature and humidity sensors (HMP60, Vaisala, Finland) with a ventilated shield. Leaf temperature was measured using a thermocouple thermometer. Photosynthetically photon flux density (PPFD) surrounding the chamber was measured using a quantum sensor (LI-190, Li-Cor, USA), where the quantum sensor was installed in another of the same transparent plastic container. The measurements were controlled by a logger (CR1000, Campbell Scientific Inc., USA), and data were recorded every second. The dilution effect due to water vapor fluctuations was corrected before calculating the photosynthetic rate (Harazono et al., 2015).

2.3 Field measurements

Leaf photosynthetic and transpiration rates were measured between 10:00 and 16:00 Alaska daylight time from late July to early August in 2016 using the open chamber system at the three sites (Table 1). Measurements were taken for sunlit leaves of

| Site ID | Species | canopy position | Chamber | C:N |
|---------|---------|-----------------|---------|-----|
| FAI     | Picea mariana          | overstory     | 8       | 15  |
|         | Betula glandulosa      | understory    | 4       | 8   |
|         | Ledum groenlandicum    | understory    | 3       | 10  |
|         | Vaccinium uliginosum   | understory    | 0       | 5   |
|         | Vaccinium vitis-idaea  | understory    | 0       | 7   |
|         | Sphagnum capillifolium | moss          | 1       | 5   |
|         | Pleurozium schreberi   | moss          | 1       | 6   |
| PFF     | Picea mariana          | understory    | 1       | 9   |
|         | Betula papyrifera      | overstory     | 2       | 16  |
|         | Populus tremuloides    | overstory     | 3       | 15  |
|         | Betula glandulosa      | understory    | 0       | 2   |
|         | Ledum groenlandicum    | understory    | 0       | 8   |
|         | Vaccinium uliginosum   | understory    | 0       | 5   |
|         | Vaccinium vitis-idaea  | understory    | 0       | 3   |
| DLS     | Picea mariana          | overstory     | 2       | 10  |
|         | Ledum groenlandicum    | understory    | 0       | 11  |
|         | Vaccinium uliginosum   | understory    | 0       | 3   |
|         | Vaccinium vitis-idaea  | understory    | 0       | 11  |

Table 1. The number of leaves used for the chamber measurements and C:N measurements.
overstory trees (Picea mariana, Betula papyrifera, and Populus tremuloides), understory shrubs (Betula glandulosa, and Ledum groenlandicum), and mosses (Sphagnum capillifolium, and Pleurozium schreberi); number of the samples are shown in Table 1. The mean air temperature within the chamber ranged from 24.2°C to 36.3°C during the study period. The measurements were conducted in sunny conditions when the PPFD was greater than 680 µmol m⁻² s⁻¹.

Photosynthetic and transpiration rates for vascular plants were measured for leaves including branches, whereas those for moss samples were measured by inserting mosses into the chamber. Mosses were sampled in a transparent vessel (4.8 × 4.8 cm² of bottom area), and the photosynthetic rate under light conditions was measured. Due to the measurement approach used, the fluxes for mosses were for ground area rather than for leaf area. Dark respiration per unit of ground area could not possibly be measured. Due to the measurement approach used, the bottom area was measured. Thus, the respiration rate of mosses under dark conditions was estimated based on Helbig et al. (1997), as two distinct relationships for the same species at different sites tended to be similar, except for Populus tremuloides. As two distinct responses were examined for Populus tremuloides, two sets of mwb and bwb were determined.

Data analysis

3.1 Ecophysiological parameters at the leaf scale

The maximum carboxylation rate per unit of leaf area (vmax) was estimated based on the one-point method (de Kauwe et al., 2016).

\[ \text{vmax} = (A_{\text{sat}} + R_{l}) \left( \frac{C_i + K_m}{C_i - \Gamma} \right) \]

where \( A_{\text{sat}} \) is the photosynthesis rate at saturating irradiances (800–1000 µmol m⁻² s⁻¹ for Picea mariana and Ledum groenlandicum; 900–1000 µmol m⁻² s⁻¹ for Betula papyrifera; 1000–1200 µmol m⁻² s⁻¹ for other species), \( C_i \) is the intercellular CO₂ concentration, \( K_m \) is the Michaelis-Menten constant, and \( \Gamma \) is the CO₂ compensation point for photosynthesis in the absence of mitochondrial respiration. \( C_i \) was estimated from the atmospheric CO₂ concentration and stomatal conductance. Assuming a temperature dependence of \( K_m \) and \( \Gamma \) (Kattge and Knorr, 2007), the maximum carboxylation at 25°C (\( v_{\text{max25}} \)) was estimated from \( v_{\text{max}} \) under different temperature conditions in the field. Stomatal conductance was estimated using the measured transpiration, leaf temperature, and vapor pressure within the chamber. \( R_{l} \) is the mitochondrial respiration in light, which is assumed to be 1.5% of \( v_{\text{max}} \) (de Kauwe et al., 2016). The \( R_{l} \) for mosses was directly measured under dark conditions, because photosynthesis of mosses was measured per unit ground area instead per unit leaf area. When directly measured \( R_{l} \) instead of assuming \( R_{l} \) to be 1.5% of \( v_{\text{max}} \), the estimated \( v_{\text{max}} \) decreased by 3.7% for Sphagnum capillifolium and 10.5% for Pleurozium schreberi.

The slope \((m_{wb})\) and intercept \((b_{wb})\) in the stomatal conductance model (Ball et al., 1987) were determined based on the leaf chamber measurements as follows:

\[ g_{sw} = \frac{A}{c_s} \frac{rh_s + b_{wb}}{c_s} \]

where \( g_{sw} \) is stomatal conductance for water vapor, \( A \) is the net photosynthetic rate, \( rh_s \) is the relative humidity at the leaf surface, and \( c_s \) is the CO₂ concentration at the leaf surface. The model parameters were determined for each plant, because the relationship for the same species at different sites tended to be similar, except for Populus tremuloides. For two distinct responses were examined for Populus tremuloides, two sets of \( m_{wb} \) and \( b_{wb} \) were determined.

3.2 Ecophysiological parameters at the ecosystem scale

Ecosystem-scale ecophysiological parameters were estimated based on the optimization of the iBILM-EC model (Ueyama et al., 2016). The sun/shade radiation transfer (de Pury and Farquhar, 1997) was included in the current version (version 2) of the model. The model was driven with environmental and micrometeorological data, including air temperature, relative humidity, PPFD, and LAI to predict gross primary productivity (GPP) and transpiration. In this study, the model was optimized using eddy-covariance-based GPP and transpiration using the
SCE-UA method (Duan et al., 1992). The optimized ecophysiological parameters were four big-leaf parameters: the maximum carboxylation rate at 25°C ($V_c^{\text{max25}}$; Farquhar et al., 1980), a maximum electron transport rate at 25°C ($J_{\text{max25}}$), and $m_{\text{ls}}$ and $b_{\text{ls}}$ in the stomatal conductance model (Ball et al., 1987). The parameterization of the photosynthesis model was based on Katge and Knorr (2007), which was the same parameterization as for the one-point method in section 3.1. The estimated canopy-scale parameters were then downscaled into units per leaf area ($V_c^{\text{max25}}$ values per leaf area) using LAI with radiation and nitrogen distribution factors (de Pury and Farquhar 1997; Lloyd et al., 2010). Further details of the model and optimization are shown in Ueyama et al. (2016).

GPP and transpiration were estimated based on the eddy covariance measurements. GPP was calculated as the difference between ecosystem respiration and net ecosystem exchange (NEE), where ecosystem respiration was estimated using the $Q_{10}$ function for air temperature (Ueyama et al., 2013, 2014a). In analyzing nighttime data, we rejected data under calm conditions using a friction velocity threshold (Ueyama et al., 2013). Transpiration was derived from the measured evapotranspiration; soil evaporation that was assumed as the potential evaporation at the forest floor (Ryu et al., 2011) was subtracted from evapotranspiration. We did not use data under wet conditions during rain and within one hour after rain. Further details regarding data preparation for the model are shown in Ueyama et al. (2016).

Comparing the ecosystem-scale parameters to the leaf-scale measurements, the optimized ecosystem-scale-parameters parameters were averaged during the mid-summer period from mid-July to mid-August, when the chamber measurements were conducted. For DLS, available data from the eddy covariance measurements were limited from 2002 to 2004 (Randerson et al., 2006; Welp et al., 2007). We used the mean of the ecosystem-scale parameters for the mid-summer period from 2002 to 2004 for DLS.

The LAI was estimated based on field observations and satellite remote sensing. For FAI and PFF, the LAI was measured using a plant canopy analyzer (LAI-2000, Li-Cor, USA), showing 1.7 m² m⁻² for FAI and 1.9 m² m⁻² for PFF from mid-July to mid-August (Ueyama et al., 2014a; Iwata et al., 2013). The LAI for DLS was estimated based on a relationship between enhance vegetation index (EVI) derived from the Moderate Resolution Spectroradiometer (MODIS) and the LAI at FAI, which was 2.5 m² m⁻² from mid-July to mid-August (Ueyama et al., 2016).

Comparing the leaf-scale $V_c^{\text{max25}}$ with ecosystem-scale $V_c^{\text{max25}}$ derived from the model optimization, the leaf-scale $V_c^{\text{max25}}$ was upscaled to scales of overstory and understory using the leaf C:N ratio. Based on a significant linear relationship between the leaf C:N ratio and measured $V_c^{\text{max25}}$ (shown in section 4.1), the ecosystem-scale overstory and understory $V_c^{\text{max25}}$ were calculated using the leaf C:N ratio measured for overstory and understory species at each site. The dominant overstory for FAI and DLS was Picea mariana, whereas the dominant overstory species for PFF were Betula papyrifera and Populus tremuloides.

4. Results

4.1 Leaf scale measurement

Across vascular plants, the measured $V_{c^{\text{max25}}}$ was lowest for Picea mariana, and the $V_{c^{\text{max25}}}$ values for Betula papyrifera and Populus tremuloides were the highest (Fig. 1; Table 2). The values of $V_{c^{\text{max25}}}$ for the other two understory species (Betula glandulosa and Ledum groenlandicum) were in the middle of these two ranges. The values of $V_{c^{\text{max25}}}$ for mosses (Sphagnum capillifolium and Pleurozium schreberi) were lower than those for the vascular plants.

The variations in the measured $V_{c^{\text{max25}}}$ of the different vascular plants were explained by the leaf C:N ratios ($R^2 = 0.68$, $p < 0.01$, $n = 18$; Fig. 1a), except for one Picea mariana sample.
The relationship to the leaf C:N ratio was clearer than that to leaf nitrogen content (Fig. 1b), where the leaf nitrogen content was estimated from the leaf C:N ratios using specific leaf area from literatures (Bond-Lamberty et al., 2002; Kloeppel et al., 1998; Table 2). The low \( \text{VC}_{\text{max}25} \) in Picea mariana was explained by high C:N ratio, whereas the high \( \text{VC}_{\text{max}25} \) values in Betula papyrifera and Populus tremuloides were explained by the low C:N ratio. In contrast, the measured \( \text{VC}_{\text{max}25} \) values for mosses were lower than those expected from the relationship.

### 4.2 Ecosystem scale comparison

The ecosystem-scale \( \text{VC}_{\text{max}25} \) from the eddy covariance data was comparable to the upscaled leaf-scale \( \text{VC}_{\text{max}25} \) using leaf C:N ratios (Fig. 2). The ecosystem-scale \( \text{VC}_{\text{max}25} \) was similar to values of understory \( \text{VC}_{\text{max}25} \) for FAI (open canopy forest), reflecting greater contributions of the understory to canopy photosynthesis. In contrast, the ecosystem-scale \( \text{VC}_{\text{max}25} \) for DLS was smaller than the \( \text{VC}_{\text{max}25} \) of the overstory and understory for this site (closed canopy forest). This result was possibly due to overestimates of the input LAI for the model, because the LAI in DLS was estimated using satellite data. The ecosystem-scale \( \text{VC}_{\text{max}25} \) was similar to the understory \( \text{VC}_{\text{max}25} \) in PFF. This result indicates that the understory greatly contributed to canopy photosynthesis in the early succession at PFF. Among the three sites, the estimated understory \( \text{VC}_{\text{max}25} \) was similar (39–47 \( \mu \)mol m\(^{-2}\) s\(^{-1}\)), although the canopy structure and vegetation composition differed.

Stomatal conductance parameters, \( \text{mb}_b \), were compared among the leaf chamber and ecosystem-scale estimations (Table 2). Based on the chamber measurement, the \( \text{mb}_b \) ranged from 5.7 to 15.6 in FAI (Table 2), which were consistent with values for the ecosystem scale (10.0). The optimized \( \text{mb}_b \) was greater than those for overstory by the leaf scale measurements in DLS and PFF. A precise comparison could not be made due to lack of measurements for the understory in the DLS and PFF sites.

### Table 2. Measured maximum carboxylation rate standardized at 25°C (\( \text{VC}_{\text{max}25}; \mu \text{mol m}^{-2} \text{s}^{-1} \)), slope (\( \text{mb}_b \)) and intercept (\( \text{bb}_b \)) of the stomatal conductance model (Ball et al., 1987), C:N ratio in leaves that were measured by the chamber, specific leaf area (SLA; \( \text{m}^2 \text{kg}^{-1} \text{dry weight} \)), nitrogen content (\( N_c; \text{g m}^{-2} \)), carbon content per dry weight (\( C_w; \text{g g}^{-1} \)), C:N ratio in leaves of all samples whose photosynthesis were measured and not measured by the chamber, and upcaled \( \text{VC}_{\text{max}25} \) based on the relationship examined in Fig. 1 and that predicted by the iBLM-EC model.

| Site ID | Species / Model canopy position | \( \text{VC}_{\text{max}25} \) | \( \text{mb}_b \) | \( \text{bb}_b \) | C:N | SLA* | \( C_w \) | \( \text{VC}_{\text{max}25} \) |
|---------|--------------------------------|-----------------|---------|---------|-----|------|--------|-----------------|
| FAI     | Picea mariana overstory        | 26.2            | 9.6     | 5.7     | 0.4 | 0.02 | 0.00   | 49.6            |
|         | Betula glandulosa understory    | 58.3            | 6.4     | 7.2     | 2.1 | 0.07 | 0.04   | 26.3            |
|         | Ledum groenlandicum understory  | 47.8            | 16.8    | 15.6    | 3.0 | 0.02 | 0.20   | 40.3            |
|         | Vaccinium uliginosum understory | 15.8            | 2.7     | 5.5     | 0.4 | -0.02| 0.03   | 15.1            |
|         | Vaccinium vitis-ideae understory| 89.6            | 10.0    | 14.6    | 7.2 | 0.4  | -0.04  | 1.3             |
|         | Pleurozium schreberi moss      | 38.1            | 4.6     | 10.0    | 4.6 | 0.04 | 0.11   | 38.1            |
|         | Picea mariana Canopy (iBLM-EC) | 15.8            | 5.7     | 0.4     | 0.0 | 0.0  | 0.03   | 15.8            |
|         | Betula papyrifera overstory    | 66.7            | 9.9     | 6.7     | 1.4 | 0.02 | 0.05   | 15.1            |
|         | Populus tremuloides overstory  | 70.5            | 2.7     | 5.5     | 0.9 | 0.05 | 0.03   | 20.5            |
|         | Betula glandulosa understory    | 58.3            | 6.4     | 7.2     | 2.1 | 0.07 | 0.04   | 26.3            |
|         | Ledum groenlandicum understory  | 47.8            | 16.8    | 15.6    | 3.0 | 0.02 | 0.20   | 40.3            |
|         | Vaccinium uliginosum understory | 15.8            | 2.7     | 5.5     | 0.4 | -0.02| 0.03   | 15.1            |
|         | Vaccinium vitis-ideae understory| 89.6            | 10.0    | 14.6    | 7.2 | 0.4  | -0.04  | 1.3             |
|         | Picea mariana Canopy (iBLM-EC) | 15.8            | 5.7     | 0.4     | 0.0 | 0.0  | 0.03   | 15.8            |
|         | Betula papyrifera overstory    | 66.7            | 9.9     | 6.7     | 1.4 | 0.02 | 0.05   | 15.1            |
|         | Populus tremuloides overstory  | 70.5            | 2.7     | 5.5     | 0.9 | 0.05 | 0.03   | 20.5            |
|         | Betula glandulosa understory    | 58.3            | 6.4     | 7.2     | 2.1 | 0.07 | 0.04   | 26.3            |
|         | Ledum groenlandicum understory  | 47.8            | 16.8    | 15.6    | 3.0 | 0.02 | 0.20   | 40.3            |
|         | Vaccinium uliginosum understory | 15.8            | 2.7     | 5.5     | 0.4 | -0.02| 0.03   | 15.1            |
|         | Vaccinium vitis-ideae understory| 89.6            | 10.0    | 14.6    | 7.2 | 0.4  | -0.04  | 1.3             |
|         | Picea mariana Canopy (iBLM-EC) | 15.8            | 5.7     | 0.4     | 0.0 | 0.0  | 0.03   | 15.8            |

* Parameters were determined for each plant, because the relationship for the same species at different sites tended to be similar, except for Populus tremuloides.

* Leaf C:N ratios for leaves that the photosynthesis measurement was conducted.

* SLA data from Kloeppel et al. (1998) for Picea mariana and Bond-Lamberty et al. (2002) for other species was used for calculating \( N_c \).

* The mean of all samples that were used and not used for the photosynthesis measurements.

* Based on the leaf C:N ratio, the \( \text{VC}_{\text{max}25} \) predicted using a relationship between the leaf C:N ratio and measured \( \text{VC}_{\text{max}25} \) (Fig. 1).

* The eddy covariance data from the past study (Welp et al., 2007) from 2002 to 2004 were used.

* No significant relationship was obtained.
5. Discussion

The leaf C:N ratio, thus leaf nitrogen content, was strongly related to the carboxylation capacity at the leaf, and thus to the photosynthetic capacity under light saturation conditions (Fig. 1). The relationship indicates that the nitrogen cycle was strongly coupled to the carbon cycle in boreal forests (Chapin et al., 2005) potentially stimulate photosynthesis (Euskirchen et al., 2010; Ueyama et al., 2009). Although the linearity was stronger in using C:N ratio than nitrogen content, superiority of C:N ratio is not conclusive because specific leaf area for calculating nitrogen content was referred from previous literatures.

The inter- and within-species variations in leaf C:N ratio and $v_{\text{max}25}$ showed that each plant had a small within-species variability of leaf C:N ratio and $v_{\text{max}25}$ (Fig. 1). Despite different soil characteristics, such as the burned upland (PFF) and bog on permafrost (FAI), the variations in $v_{\text{max}25}$ of Picea mariana among ecosystems were smaller than the inter-species variation. The small within-species variability of the photosynthetic capacity in Picea mariana infers that the potential increases in $v_{\text{max}}$ of Picea mariana could be small due to their small plasticity, even if N availability increases. This result may be consistent with a finding that recent warming decreased the radial ring growth of Picea mariana trees (Beck et al., 2011), which could be caused by competitive advantage of productive understory plants. The decreased contribution in Picea mariana could increase the ecosystem-scale $v_{\text{max}25}$ due to increased contributions of the understory.

The small within-species variability of the leaf C:N ratio and $v_{\text{max}25}$ suggests that the future increase in canopy photosynthesis due to increased N availability could be associated with changes in canopy structure and species composition. Increased N availability could favor a productive understory rather than increased photosynthesis of Picea mariana, as discussed above. Changes in species composition in adapting to higher nutrient environments were reported as an important process in arctic tundra (Shaver et al., 2001). The structural changes could influence canopy photosynthesis in addition to changes in the LAI (McMillan and Goulden, 2008).

The carboxylation capacity of mosses was considerably lower than those expected from low C:N ratio (Fig. 1). This was because allocation of nitrogen to photosynthetic tissues differed to those for vascular plants (Rice et al., 2008). Rice et al. (2008) reported that nitrogen content only for capitulum correlated to photosynthetic rates; we measured C:N ratio for whole shoot system rather than capitulum. The high C:N ratios for mosses were partly because the $v_{\text{max}25}$ values for mosses were measured per unit of ground area instead of per unit of leaf area; photosynthesis in low moss layers did not possibly meet light saturation conditions.

The measured leaf-scale parameters, $v_{\text{max}25}$, and $m_{\text{sb}}$ were comparable to previous studies at boreal forests in North America. The measured $v_{\text{max}}$ for Picea mariana were within the range of those previously reported at a non-permafrost soil in Canada (8.5–50 $\mu$mol m$^{-2}$ s$^{-1}$; Dang et al., 1998; Cai and Dang, 2002). The measured $v_{\text{max}}$ were smaller than those measured at a temperate region in Wisconsin, USA for Betula papyrifera (84 $\mu$mol m$^{-2}$ s$^{-1}$; Uddling et al., 2009) and Populus tremuloides (76 $\mu$mol m$^{-2}$ s$^{-1}$; Uddling et al., 2009), but similar to those reported at a non-permafrost soil, Canada (50–60 $\mu$mol m$^{-2}$ s$^{-1}$; Cai and Dang, 2002). The values for Sphagnum and Pleurozium mosses (5–14 $\mu$mol m$^{-2}$ s$^{-1}$; Williams and Flanagan, 1998) were consistent with our study, but a higher $v_{\text{max}}$ of 78 $\mu$mol m$^{-2}$ s$^{-1}$ was reported for Ledum groenlandicum in Canada (Bubier et al., 2011). The values of $m_{\text{sb}}$ were within a range reported in previous measurements (4–16; Ball et al., 1987; Medlyn et al., 2011), except for mosses that do not have stomata and passively control gas diffusion according to different water conditions (Williams and Flanagan, 1998).

Steps toward improving the canopy photosynthesis model were suggested in this study. First, the measured difference in nitrogen content and $v_{\text{max}25}$ between overstory and understory differed from the concept that the photosynthetic capacity was positively correlated to light availability within a canopy (e.g., Lloyd et al., 2010). Greater photosynthetic capacity of the understory could be characteristic of boreal forests in interior Alaska (Ikawa et al., 2015). Modification of the vertical nitrogen
distribution factor (Lloyd et al., 2010) for boreal forests could improve the predictive accuracy of the model. Second, the values of \( m_{\text{thb}} \) should be evaluated with the leaf- and ecosystem-scale measurements. The measured leaf-scale \( m_{\text{thb}} \) differed among the plants, and the estimated ecosystem-scale \( m_{\text{thb}} \) varied among the ecosystems (Table 2). Upscaling \( m_{\text{thb}} \) considering within-canopy variations improves the predictive accuracy of the model. Further leaf-scale measurements of \( m_{\text{thb}} \), including moss species and development of the upscaling method, are required in future studies. Evaluating the water use efficiency at the leaf and ecosystem scales could help provide precise estimates of CO2 and water vapor fluxes.

6. Conclusion

Evaluating the ecophysiological parameters via ecosystem- and leaf-scale measurements was useful for improving canopy photosynthesis models and understanding the ecophysiology in boreal forests. The ecosystem-scale photosynthetic parameters were influenced by canopy structure and species composition, such as different contributions of the overstory and understory within a canopy. This finding indicates that appropriate modeling of overstory and understory improves the accuracy in simulations of the carbon cycle in boreal forests in interior Alaska. The strong linkage between the leaf C:N ratio and photosynthetic capacity also indicates that modeling the nitrogen cycle is important for predicting the carbon cycle. A precise understanding is necessary to evaluate how the canopy structure and species composition change with increased N availability due to high-latitude warming.

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