Eurasian J. For. Res. 1: 31-37 , 2000


# Photosynthetic Characteristics of Dahurian Larch, Scotch Pine and White Birch Seedlings Native to Eastern Siberia Raised Under Elevated $CO_2$

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## Abstract

Growth pattern and biomass production of trees will be affected by increasing atmospheric $CO_2$, which may change the vegetation pattern in eastern Siberian where continuous permafrost is present. In this phytotron experiment, effects of enriched $CO_2$ on the shoot growth and photosynthetic parameters were examined to predict future regeneration capacity of major tree species in the permafrost region. The leader shoot of larch and white birch ceased to grow at 80-90 days after leaf unfolding, by contrast, Scotch pine stopped to shoot elongation at ca. 35 days. Growth cessation of seedlings raised under 70 $PaCO_2$ (high $CO_2$) was one week later as compared to seedlings grown under 36 $PaCO_2$ (ambient $CO_2$). Leaf area of white birch raised under high $CO_2$ was smaller than that at ambient $CO_2$, while there was no difference in needle size of larch and Scotch pine grown under both $CO_2$ levels. Specific leaf area (SLA) deceased in all species raised under elevated $CO_2$. There was no significant difference in the photosynthetic rate of the two conifers grown at high and ambient $CO_2$ levels. The photosynthetic rate in white birch measured at the growth $CO_2$ level showed almost the same value, which was considered as homeostatic adjustment. The apparent quantum yield and carboxylation efficiency of larch and white birch raised under high $CO_2$ decreased, while those of Scotch pine showed no difference. Instantaneous value of water use and nitrogen use efficiency in all seedlings raised in enriched $CO_2$ increased especially for Scotch pine. Based on these results, we infer that, in a future elevated $CO_2$ condition, the larger increase in water use efficiency of Scotch pine could enhance its dominance the forest of eastern Siberia region.

*Key words*: Eastern Siberia, Dahurian larch, Scotch pine, white birch, elevated $CO_2$

## Introduction

Larch species (*Larix gemlinii* and *Larix cajanderi*) are broadly distributed in the eastern Siberian permafrost region (Gower and Richards 1989, Schulze *et al.* 1995, Abaimov 1998) and is sometimes associated with Scotch pine and white birch depending on the depth of active soil layer and the degree of disturbance (Ohta *et al.* 1993). Growth and development of these species are strongly affected by the lack or increased precipitation and increasing temperature. However, with the increasing atmospheric $CO_2$ and a 4 – 5°C rise in mean temperature predicted in near future, young tree stands in this region could become a major carbon sink (Mooney *et al.* 1991, Ceulemans *et al.* 1999). A major tree species in eastern Siberia is Dahurian larch which is characterized by its high photosynthetic rate (Fry and Phillips 1976, Koike *et al.* 2000). Moreover, Scotch pine and white birch are expected to become $CO_2$ sink because of their high growth rate with light demanding characteristics (Kuusela 1990). In the condition of increasing $CO_2$ levels, it is important to evaluate the growth and regeneration capacity of representative tree species native to this continuous permafrost region (Fukuda 1996, Koike *et al.* 1998).

The preferred habitat of Dahurian larch (*Larix gmelinii*), Scotch pine (*Pinus sylvestris*) and white birch (*Betula platyphylla*) is mesic, xeric and slightly xeric condition, respectively (Ohta *et al.* 1993). But all species are light demanding, especially in white birch that invades disturbed areas (Koike *et al.* 1996). How will water and nutrient demands directly related to water use and nitrogen use efficiency in the three species alter in a future "greenhouse" environment? Growth response of white birch to elevated $CO_2$ may be the quickest because of its early successional traits, followed by Dahurian larch and Scotch pine (Kuusela 1990, Schulze *et al.* 1994). It is assumed that the change in growth and regeneration capacity of tree species under

(Received; Mar.15, 2000: Accepted; June 16, 2000)
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elevated $CO_2$ would be expressed through the present pattern of shoot growth (e.g. free or fixed growth type) and of water use efficiency or nitrogen use efficiency.

To test the assumption that Scotch pine may increase water use efficiency and white birch would improve nitrogen use efficiency, we raised seedlings of the three species under a doubling of present $CO_2$ level and an increase of ambient temperature by 4°C in order to evaluate the potential growth and acclimation capacity of these species. We discussed the growth responses of these seedlings in relation to their simulated future growth habitat. Based on these, we inferred a plausible vegetational change in eastern Siberia.

## Materials and Methods

**1. Plant materials:** Dahurian larch (*Larix gmelinii*), Scotch pine (*Pinus sylvestris*) and white birch (*Betula platyphylla*) seeds were collected from the vicinity of Yakutsk city (62°N, 129°E). Seeds were stored at 10°C until germination. Except for larch, seeds were sown on sandy soil without nutrients. Larch seeds could germinate under a layer of wet "peat plate" of 3 cm thick as a seedbed (Kohnoen Co Ltd., Sapporo, Japan). After germination, seedlings were grown under ambient $CO_2$, day/night temperature of 26/12°C with 20 hours day-length with supplemental light of 500 W incandescent lamps. Seedlings were supplied with 100 mg.liter$^{-1}$ of nitrogen with enough water once weekly. When seedling height reached ca. 3 cm for Dahurian larch and white birch, and ca. 5 cm for Scotch pine, all species were transplanted to 2.6 liter (dm$^3$) pots filled with clay soil mixed with the Kanuma pumice soil (3: 1 in volume).

**2. Treatments:** Potted seedlings were placed in two growth cabinets (Koito KG type , Yokohama, Japan) exposed to natural light. Day length increased with supplemental lighting (Incandescent lamps, 500 W, National, Tokyo, Japan) between 0300 - 0700 and 1800 - 2300 hr JST to maintain a 20-hr daylight consistent with the summer day length at Yakutsk. Each cabinet received a regulated level of $CO_2$ at 36 Pa $CO_2$ and 70 Pa $CO_2$, respectively. The ambient temperature in the cabinets was kept 26/12°C (light/dark) which simulate the predicted 4°C increase in mid-21 century there. Nutrient was supplied at 100 mgN per pot per week with enough water.

There was no chamber replication at each $CO_2$ level because of the limited number of chambers. Thus, growth cabinets for $CO_2$ treatment of high and ambient $CO_2$ treatments were switched each other to reduce possible bias from inconsistencies in environmental conditions between cabinets. Pot positions were shuffled in the cabinet once a week to reduce the position effect within the chamber.

**3. Measurements:** Shoot length was measured at one-week intervals. Gas exchange rate was measured at the fixed temperature of 26°C (daytime growth temperature) with a portable gas analyzer (ADC H3, U.K.). For measurement of each photosynthetic parameter, more than four seedlings per species of each treatment were used. For Scotch pine, current year needles were used for the measurement because they developed in the growth cabinet (future condition). Therefore, gas exchange measurements were carried out with newly formed leaves under high and ambient $CO_2$ treatments in all species. Needle surface area was measured with a digitizer and a computer. Needle area was expressed as total surface area because stomata of needle were arranged in nearly all surfaces. Leaf area of white birch was determined with an area meter (Hayashi-Denko AAM 8, Tokyo, Japan).

Leaf maturation was estimated by monitoring chlorophyll content in a leaf with a potable chlorophyll meter (SPAD, Minolta, Tokyo, Japan). Foliage maturation was defined as the SPAD value reached a stable value. For needle, we also applied the leaf color map (Kiuchi and Yazawa 1992) correlated with the SPAD value. Specific leaf area (SLA; cm$^2 \cdot$g$^{-1}$) was calculated as a ratio of leaf area (total surface area for conifers and single side area for white birch) to dry mass (at 85°C for 48 hrs).

The initial slope of the light - photosynthesis (Pn) relationship at saturating $CO_2$ was used to estimate quantum yield ($\Phi$); the carboxylation efficiency (CE) was derived from the Ci (intercellular $CO_2$ concentration)- photosynthesis curve, Light- and $CO_2$-saturated photosynthetic rate represents the rate of RuBP regeneration (Sharkey 1985, Sage 1994). Foliage nitrogen was determined with a N/C analyzer (Sumigraph 800NT, Sumica CO. LTD., Osaka, Japan). Water (WUE) and nitrogen use efficiency (NUE) were calculated as the ratio of Pn and transpiration, and Pn and leaf nitrogen concentration, respectively (Field and Mooney 1983).

Statistical differences among treatments and species were analyzed using the t-test.

## Results

### 1. Shoot growth

The cessation of elongation of leader shoot occurred in 80-90 days after leaf unfolding in Dahurican larch and white birch (Fig. 1). By contrast, shoot elongation in Scotch pine ceased at ca. 35 days after needle development. Growth cessation of seedlings of all species raised under high $CO_2$ was about 7 days later as compared to

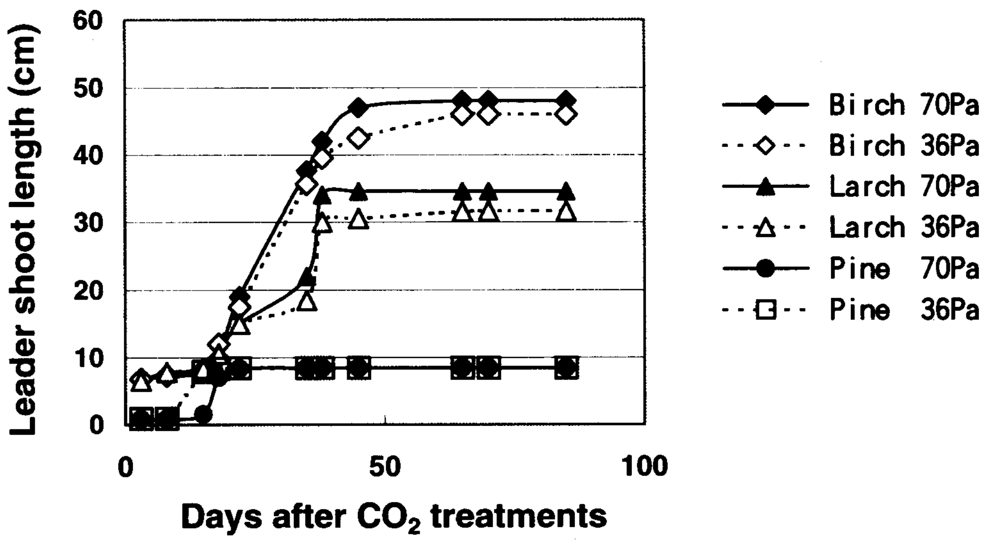


Fig. 1. Time course of shoot elongation in Dahurian larch, Scotch pine and white birch seedlings raised under different $CO_2$ levels.

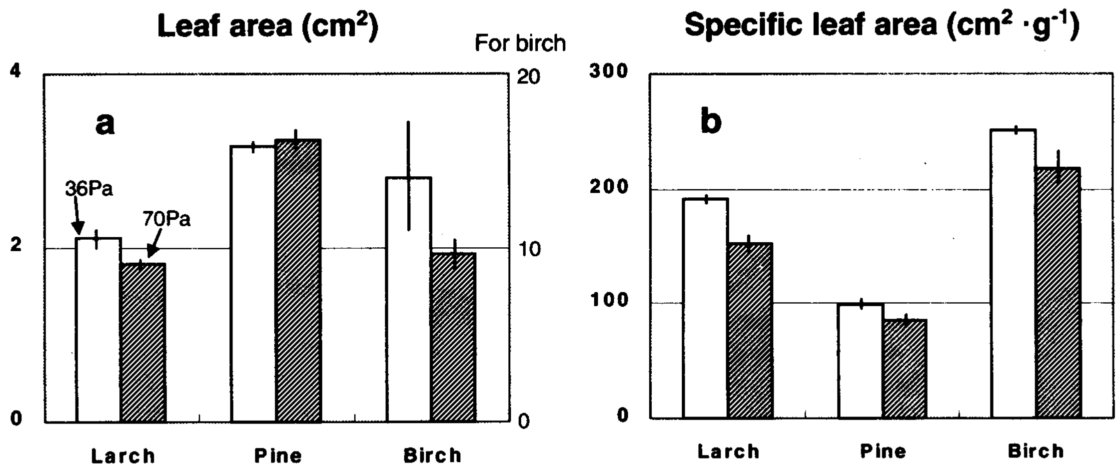


Fig. 2. Individual leaf or needle area (a) and the specific leaf area (b) of three species of seedlings raised under 36 and 70 Pa $CO_2$.
Vertical bars indicate the standard deviation, which is the same in the following figures.

the seedlings under ambient $CO_2$. Foliage of larch and white birch matured 40-50 days after the $CO_2$ application, but that of Scotch pine needle required 80 days after the treatment.

Foliage color at high $CO_2$ grown seedlings of three species was slightly yellowish as compared with seedlings grown at ambient $CO_2$ (data is not shown). Scotch pine had current and one-year old needles. Both two type of needles changed their color from dark green to yellowish green, especially in one-year old needle. Individual leaf area of larch and white birch raised under high $CO_2$ was slightly smaller than those under ambient $CO_2$ (not significant). There was no difference in needle area of Scotch pine between the $CO_2$ treatments (Fig. 2a). Specific leaf area (SLA) of all species grown under 70 Pa $CO_2$ was lower than those under 36 Pa $CO_2$. The difference in the SLA between $CO_2$ treatments for Dahurian larch and white birch was smaller ($P<0.05$), however, that for Scotch pine was statistically not significant (Fig. 2b).

## 2. Gas exchange characteristics

The trend in net photosynthesis (Pn) showed higher rates in seedlings raised at 70 Pa $CO_2$ than those at 36 Pa $CO_2$ (Fig. 3) but they were not statistically different. In white birch, Pn measured at the growth $CO_2$ concentration showed almost the same value (shown in dotted line in Fig. 3). The Pn of the two conifers was half that of white birch because the Pn of conifers was expressed as net photosynthetic rate per total surface area. If we used only the projected needle surface area of larch and Scotch pine, Pn of all species showed a similar value.

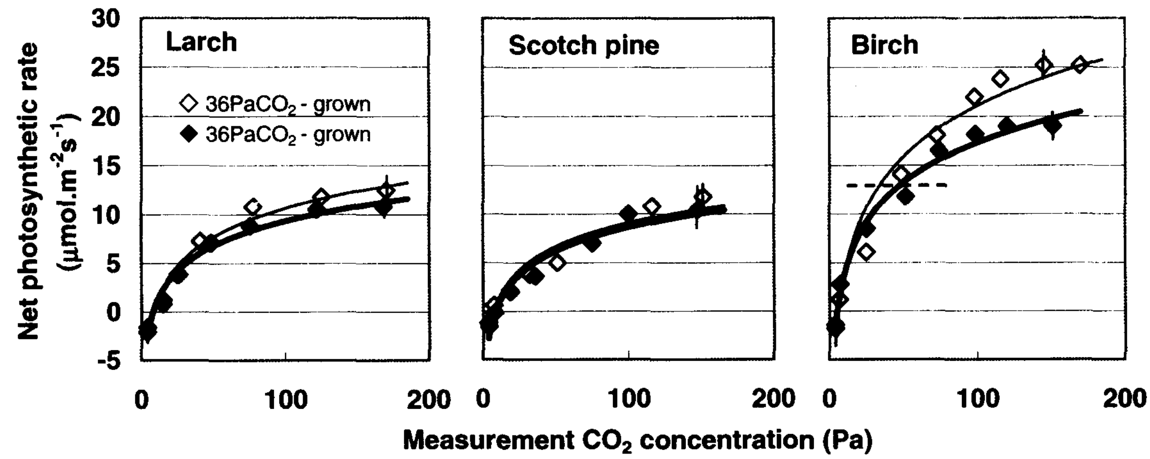


Fig. 3. Relationship between the measurement $CO_2$ and the net photosynthetic rate of three kinds of tree seedlings native to eastern Siberia raised under ambient and enriched $CO_2$.
In white birch , dotted line shows the 100% homeostatic adjustment in the photosynthetic capacity.

The quantum yield ( Φ ) of all seedlings grown at high $CO_2$ showed lower values when compared with those at ambient $CO_2$, especially for larch and white birch ($P<0.01$, Fig. 4a). However, the difference was not significant in Scotch pine seedlings. Carboxylation efficiency (CE) of larch and white birch raised under 36 Pa $CO_2$ was greater than those under 70 Pa $CO_2$ ($P<0.05$, Fig. 4b). The CE of Scotch pine seedlings showed similar activity irrespective of $CO_2$ treatment. $CO_2$- and light-saturated photosynthetic rate (Pmax) of all species raised under 70 Pa $CO_2$ tended to be slightly lower than that under 36 Pa $CO_2$ (Fig. 4c). Surface area based Pmax of both conifer species was lower compared with that of white birch seedlings grown in both $CO_2$ levels.

The water use efficiency (WUE) of all species raised under high $CO_2$ increased, especially in larch seedlings (Fig. 5a). Under the ambient $CO_2$ level, the WUE of larch was the lowest. Scotch pine and white birch had similar values of WUE which was about 1.7 times larger than that of larch seedlings under ambient $CO_2$. The nitrogen use efficiency (NUE) of all species grown under high $CO_2$ showed an increase to almost the same value (Fig. 5b). Under ambient $CO_2$, the NUE of larch seedlings had the highest value while that of Scotch pine seedlings was the lowest value. Therefore, the largest increase in the NUE at high $CO_2$ was found in Scotch pine seedlings.

## Discussion

### 1. Physiological acclimation

Seedlings raised under high $CO_2$ sometimes show a down regulation in photosynthesis (Oechel and Billings 1992, Sage 1994, Ceulemans *et al.* 1999). In the present experiment, except for white birch, net photosynthetic rate (Pn) of the two conifer seedlings grown at high $CO_2$ showed no clear down regulation (Fig. 3). These species have a light demanding growth traits (Ohta *et al.* 1993) and usually show high

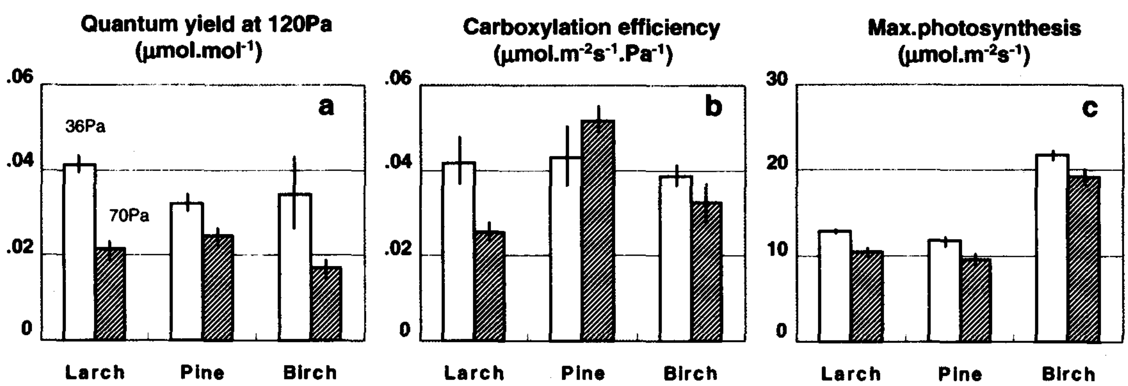


Fig. 4. The photosynthetic parameters, quantum yield (a), carboxylation efficiency (b), maximum rate of photosynthesis at $CO_2$ and light saturation (c) of three kinds of tree seedlings raised under ambient and high $CO_2$.

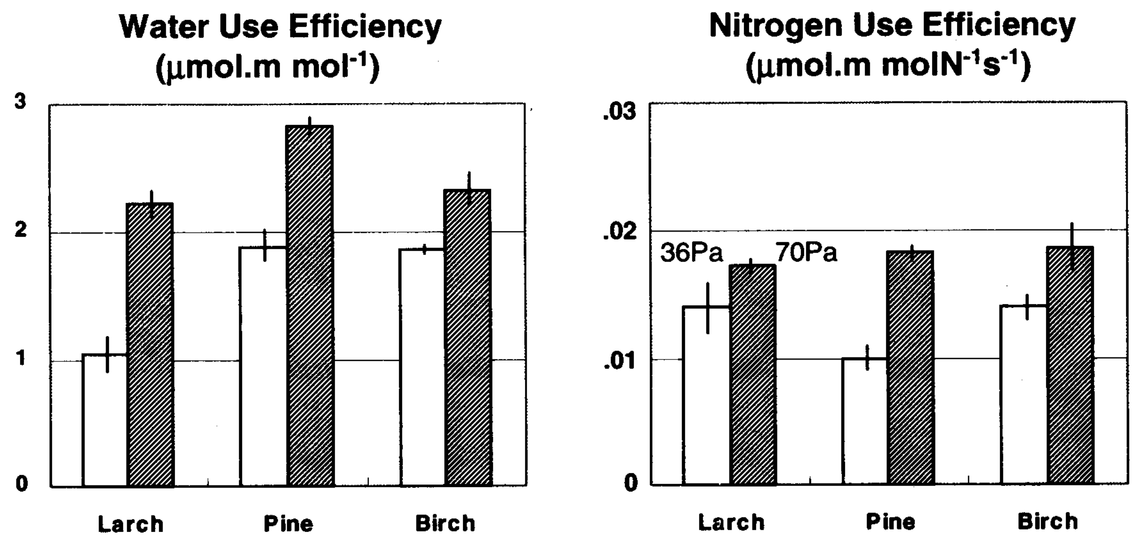


Fig. 5. Instantaneous Water use efficiency (WUE) and Nitrogen use efficiency (NUE) of seedlings grown at 36 and 70 Pa $CO_2$.

growth rate compared with several mid- and late successional tree species (Bazzaz 1996). This high growth rate usually lead to a reduction of nitrogen concentration in plant organs, especially in leaves (Coleman *et al.* 1993, Koike *et al.* 1996, Ceulemans *et al.* 1999). And because leaf N is often correlated with Pn (Field and Mooney 1983), Pn of white birch seedlings at high $CO_2$ showed lower photosynthetic rate.

Quantum yield ($\Phi$) is positively correlated with leaf chlorophyll content of less than 5mgChl.dm$^{-2}$ for deciduous broadleaved tree leaves (Koike unpublished). In this study, foliage color at high $CO_2$ grown seedlings of three species was slightly yellowish which may imply the reduction of chlorophyll which affected quantum yield. Under high $CO_2$, one possible reason for the reduction in chlorophyll may be that under high $CO_2$, the relatively high growth rate during early growth stage led to a dilution of nitrogen concentration in leaves (Coleman *et al.* 1993).

What about the regeneration capacity of tree seedlings grown under elevated $CO_2$ in future? The eastern Siberian Taiga is situated on permafrost (Archibold 1995), therefore a strong competition for water and nutrients may prevail among species and among individuals. Quantum yield stands for the utilization capacity of lower light fluxes. Under high $CO_2$, all species examined also had lower quantum yield, which may be disadvantage for seedlings under the low light flux in the forest floor. However, because of low tree density, the light environment of forest floor was relatively favorable (Kanazawa *et al.* 1993). If the development of a stand structure in the future environment would remain similar to the present, then lower quantum yield induced by high $CO_2$ may not pose a serious limitation on early seedling growth. This point (poor utilization of low light flux) of regeneration process in Taiga seems to conradict the simulation results by Oikawa (1986). He predicted that poor regeneration would occur in Tropical Rain Forest with reducing light flux because of high leaf densities of overlayer induced by high $CO_2$.

Negative feedback in growth was found in potted plants because of an imbalance of nutrients between the above-ground and below-ground components and an inefficient translocation of carbon from leaves to storage organs, especially to roots (i.e., smaller SLA with carbohydrate accumulation, Fig. 2b). There was no difference between Pn of larch and pine seedlings grown under ambient and elevated $CO_2$, which may be related to seedling size. These conifer seedlings were small enough against the pot size and may have no root restriction (McConnaughay *et al.* 1993).

The initial slope of the Pn-Ci (intercellular $CO_2$ concentration) curve represents RuBP carboxylase activity, namely carboxylation efficiency (CE) (Sharkey 1985). The CE of the three species raised under high $CO_2$ showed lower value as compared with those under ambient $CO_2$ (Fig. 4b). This means not only a reduction of specific RubisCO activity but also a decrease in total amount of RubisCO, however, the degree of this reduction appears to be species specific. Some plants reduced activities of RubisCO and some also showed a reduction in the amount of RubisCO under high $CO_2$ (Ceulemans *et al.* 1999). Further research will be needed to clarify the mechanism of negative feedback mechanisms involved under elevated $CO_2$. Further research will be needed to clarify the mechanism of negative feedback involved under elevated $CO_2$.

**2. Habitat selection under a global greenhouse environment**

Nitrogen use efficiency (NUE) of all three species increased under high $CO_2$ (Fig. 5a, b). Because larch generally prefers humid fertile conditions accompanied by alder with nitrogen fixing micro-organisms (Ohta *et al.* 1992), it may have a lower inherent NUE. In contrast, Scotch pine and white birch can survive in relatively dry and infertile conditions (Ohta *et al.* 1992) where a high NUE is important. Table 1 shows the comparison of physiological characteristics of the three representative species native to eastern Siberian Taiga raised under 70 Pa $CO_2$ and 36 Pa $CO_2$. Future performance of these species will likely depend considerably on their present habitat preferences. For example, since Scotch pine can survive under relatively poor conditions at present, under elevated $CO_2$, an improved WUE and NUE will likely enhance its growth more than the other species. Larch requires humid and fertile sites (Gower and Richards 1989) It doesn't need to have high NUE because nitrogen is not limiting where this species grows (Table 1). White birch may behave in an intermediate fashion between Dahurian larch and Scotch pine.

In a predicted greenhouse environment, a shortage of precipitation and a decrease in soil infertility is expected in the eastern Siberian area. We may find an increasing dominance of Scotch pine in this region because of its high WUE and NUE. However, nitrogen content of needles of Scotch pine was not significantly reduced by high $CO_2$. This observation may be related to the evergreen characteristics of Scotch pine where evergreen leaves usually act as a storage organ (Moore 1980) and available for translocation to newly developing organs. The retranslocation of nitrogen from senescing leaves back to the plant parts of the other species was not well revealed. Moreover, because it is not known how the permafrost layer may respond to the increasing temperature and the changing patterns of precipitation is also not well studied (Mooney *et al.* 1991). The active layer in Siberia might become deeper and last longer in the summer, further predictions of vegetation dynamics should be analyzed according to the integration of the effect of climate change on habitats and the physiological responses of individual tree species.

**Acknowledgments**

This research was conducted in the Forestry and Forest Products Research Institute (FFPRI), Hokkaido Research Center. Financial support was partly made by the Japan Environment Agency (by Dr. G. Inoue) and Japanese MESSC. Thanks are also due to Mr. T. Ueda (Hokkaido Dalton LtD) for designing the $CO_2$ controlling unit.

Table 1. A summary of growth and photosynthetic characteristics of larch, Scotch pine and white birch seedlings grown under 70 $PaCO_2$ as compared with those under 36 $PaCO_2$

| | Larch | Scotch Pine | White birch |
|---|---|---|---|
| Pmax | small decrease | small decrease | small decrease |
| CE | large decrease | no change | small decrease |
| Φ | large decrease | decrease | large decrease |
| WUE | increase | increase | small increase |
| NUE | small increase | increase | increase |
| Homeostatic adjustment | small increase | small | large |

Notes: Pmax ($\mu$ $mol.m^{-2}s^{-1}$): Net photosynthetic rate at the saturated $CO_2$ and light,
CE: ($\mu$ $mol.m^{-2}s^{-1}Pa^{-1}$) carboxylation efficiency (an initial slope of Ci-net photosynthetic rate),
Φ ($mol.mol^{-1}$): Initial slope of PPFD and net photosynthetic rate at $CO_2$ saturation,
WUE: ($\mu$ $mol.mmol^{-1}$): Water use efficiency and NUE ($\mu$ $mol.mmolN^{-1}s^{-1}$): Nitrogen use efficiency.
"Homeostatic adjustment" means the physiological adjustment of net photosynthetic rate measured at the same $CO_2$ levels of plants grown under different $CO_2$ concentration.

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