

Leaf conductance and CO₂ assimilation of *Larix gmelinii* growing in an eastern Siberian boreal forest

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Summary In July 1993, we measured leaf conductance, carbon dioxide (CO₂) assimilation, and transpiration in a *Larix gmelinii* (Rupr.) Rupr. ex Kuzen forest in eastern Siberia. At the CO₂ concentration of ambient air, maximum values (mean of 10 highest measured values) for CO₂ assimilation, transpiration and leaf conductance for water vapor were 10.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 3.9 $\text{mmol m}^{-2} \text{s}^{-1}$ and 365 $\text{mmol m}^{-2} \text{s}^{-1}$, respectively. The corresponding mean values, which were much lower than the maximum values, were 2.7 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 1.0 $\text{mmol m}^{-2} \text{s}^{-1}$ and 56 $\text{mmol m}^{-2} \text{s}^{-1}$. The mean values were similar to those of *Vaccinium* species in the herb layer. The large differences between maximum and actual performance were the result of structural and physiological variations within the tree crowns and between trees that reduced maximum assimilation and leaf conductance by about 40 and 60%, respectively. Thus, maximum assimilation and conductance values averaged over the canopy were 6.1 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 146 $\text{mmol m}^{-2} \text{s}^{-1}$, respectively. Dry air caused stomatal closure, which reduced assimilation by an additional 26%. Low irradiances in the morning and evening had a minor effect (–6%). Daily canopy transpiration was estimated to be 1.45 mm day^{-1} , which is higher than the value of 0.94 mm day^{-1} measured by eddy covariance, but similar to the value of 1.45 mm day^{-1} calculated from the energy balance and soil evaporation, and less than the value of 2.1 mm day^{-1} measured by xylem flux. Daytime canopy carbon assimilation, expressed on a ground area basis, was 0.217 $\text{mol m}^{-2} \text{day}^{-1}$, which is higher than the value measured by eddy flux (0.162 $\text{mol m}^{-2} \text{day}^{-1}$ including soil respiration). We discuss the regulation of leaf gas exchange in *Larix* under the extreme climatic conditions of eastern Siberia (temperature > 35 °C and vapor pressure deficit > 5.0 kPa).

Keywords: canopy CO₂ assimilation, eastern Siberia, leaf CO₂ assimilation, transpiration, *Vaccinium*.

Introduction

The climate of the boreal forests of eastern Siberia, which are dominated by deciduous *Larix gmelinii* (Rupr.) Rupr. ex Kuzen trees, resembles that of a boreal desert during long periods of the growing season. In summer, daytime air temperatures regularly exceed 30 °C and vapor pressure deficits reach more than 3.0 kPa so that the seasonal potential evaporation rate of 460 mm exceeds the summer rainfall of about 200 mm (Kelliher et al. 1997), and soils reach freezing temperatures at about 0.7 m depth in summer (Utkin 1965, Schulze et al. 1995). Although these conditions are unusual for growth of mesomorphic deciduous leaves (Gower and Richards 1990), it is estimated that the deciduous conifer *Larix gmelinii* covers an area in eastern Siberia that is between 1 million km² (manageable forest of East Siberia, Shvidenko and Nilsson 1994) and 3.5 million km² (total area of distribution including transition to tundra, Abaimov et al. 1980). Because of the vastness of the boreal forests of eastern Siberia, it has been postulated that the photosynthetic assimilation of these forests may significantly contribute to the carbon sink of the northern latitudes (Jarvis and Dewar 1993). Despite the large area in the boreal zone of eastern Siberia that is forested with *Larix gmelinii*, there are no data available on leaf conductance and leaf photosynthetic capacity of this dominant forest species. In contrast, measurements have been made on other *Larix* species with a much narrower range of distribution (Gower and Richards 1990). Few data are also available for the western Siberian *Larix sibirica* Ledeb. Lvs. (Sherbatyuk et al. 1991), which is genetically distinct from *L. gmelinii*.

We estimated maximum rates and the daily balance of carbon assimilation, and leaf conductance, and the variation of gas exchange within and between tree crowns. We also examined the way in which *Larix* regulates its carbon and water relations under such extreme climate conditions.

Materials and methods

Measurements were carried out in 125-year-old stands of *Larix gmelinii*, growing on alluvial silt loam over limestone, located 160 km south of the city of Yakutsk, Siberian Russia, and about 50 km from the next human settlement (60°51' N, 128°16' E, 300 to 350 a.s.l.). The study site (Table 1) has been described in detail by Schulze et al. (1995). Maximum stand height is 20.5 m, which is almost twice the mean tree height as a result of the large number of subdominant and suppressed trees. Leaf area index (LAI determined by harvest, Schulze et al. 1995) is only 1.4, despite a high tree density. The low leaf and crown cover allow for a dense Ericaceous ground cover of *Vaccinium* spp. The litter and humus layer contained 8.8 mol N m⁻²; a small pool size of N compared with the 1.2 mol N m⁻² immobilized in aboveground biomass. Tree growth in this ecosystem is strongly constrained by availability of N, and a natural fire sequence is necessary for reestablishment of the forest and its N cycle (Schulze et al. 1995).

A tower was erected at the site to access branches of four trees at the top of the canopy. Measurements were carried out on 15 branches in the sun-crown at 18 m height (3–4 per tree), and 12 branches in the shade-crown (3–5 per tree at 8 m height), on shade trees close to the forest floor, and on understory *Vaccinium* species. Daily time courses were measured in the middle section of a twig, enclosing 3–4 short shoots. Measurements were also made along the main axis of four twigs (current-year and older parts of twigs).

During midsummer from July 14 to 29, 1993, CO₂ gas exchange, leaf conductance and transpiration were measured on fully developed needles with an LI-6200 porometer (Li-Cor, Inc., Lincoln, NE). Although care was taken to maintain the assimilation chamber of the porometer in the shade, chamber temperatures increased 4 to 6 °C above ambient tempera-

ture with associated effects on vapor pressure deficit (VPD) in the porometers during some measurements. It was not possible to measure leaf temperatures of *Larix* needles accurately in the porometer, but the difference between air and needle temperatures was assumed to be small because the chamber was well ventilated. It is possible that higher temperatures occurred near the base of a fascicle of needles growing on a short shoot; however, *Larix* needles lack stomata near the petiole. Vapor pressure deficits were calculated on the basis of relative humidity and chamber air temperature measured next to the fascicle.

We compared our data with canopy conductances derived from xylem flux measurements (Arneeth et al. 1996), which seems a reasonable comparison for a canopy of high aerodynamic conductance ($G_a = 100$ to 200 mm s⁻¹ for a horizontal wind speed of 1 to 2 m s⁻¹, Kelliher et al. 1997). The highest conductance value obtained with the LI-6200 (366 ± 16 mmol m⁻² s⁻¹, $n = 10$ highest values) was about 20% higher than the value calculated from xylem flux measurements (300 mmol m⁻² s⁻¹).

All results are expressed on the basis of projected needle area which was measured with a leaf area meter from photocopies of needles. These copies were taken in the field with light sensitive paper (Ozalit-paper, Agfa P90, Frankfurt, Germany) for all needles that were enclosed in the porometer chamber. For the copying procedure needles were flattened by a glass cover.

Results

Larix gmelinii is a deciduous conifer with short shoots consisting of bundles of 15 to 30 needles varying from 5 to 20 mm in length. The needles are densely packed at their basal end where they emerge from the short shoot (Figure 1A). Needle anatomy (Figure 1B) is characterized by a thick epidermis, which is reinforced by several layers of sclerenchymatic cells. There are two rows of stomatal cells on the abaxial-side and two double rows on the adaxial-side of the needle with about 10 stomatal cells per mm length on each row. Thus, a 10-mm-long needle may have only 600 stomata (30 stomata per mm² needle surface area). Shade needles lack the outer stomatal rows and stomatal density decreases to about 20 stomata mm⁻², which is similar to *Larix decidua* Mill. (Meidner and Mansfield 1968). The basal end of the needle (about 1.5 mm) has no stomatal cells. The stomatal aperture may reach 20 μm in length and 1 μm in width (measured in a fully hydrated microscopic longitudinal section of the epidermis), which is similar to measurements on *Larix decidua* (Meidner and Mansfield 1968). The scleromorphic epidermis contrasts to a very spongy mesophyll that connects a thin layer of palisade cells with the endodermis. The cells in the central mesophyll are arranged as horizontal rows separated by large air spaces (Figure 1C).

Larch needles show a considerable range in size and thickness within one fascicle and between fascicles depending on the position along the main branch or twig. The mean needle weight per projected area was 138 ± 6 (SE) g m⁻² ($n = 26$ fascicles), with minimum needle weights per area in the shade

Table 1. Characteristics of the *Larix gmelinii* study site. Values are means ± SE, and number of samples is in brackets.

Parameter	Value
Age (years)	125 ± 8 (16)
Maximum tree height (m)	20.5
Mean tree height (m)	12.3 ± 0.9 (500)
Leaf area index (m ² m ⁻¹)	1.5
Crown cover (%)	89
Stem number (ha ⁻¹)	1960
Basal area (m ² ha ⁻¹)	23.5
Leaf nitrogen concentration (mg g ⁻¹)	15.6 ± 0.2
Total/projected needle area (m ² m ⁻²)	2.59
Mass per leaf area (g m ⁻²)	137.9 ± 6
Depth of L + Ah horizon (mm)	80
Dominant ground cover species	<i>Vaccinium vitis idaea</i> L. <i>Vaccinium uliginosum</i> L. <i>Arctostaphylos uva-ursa</i> (L.) K. Spreng. <i>Arctous erythrocarpa</i> Small
Dominant shrubs	<i>Alnaster fruticosa</i> L. <i>Betula platyphylla</i> Sukachev

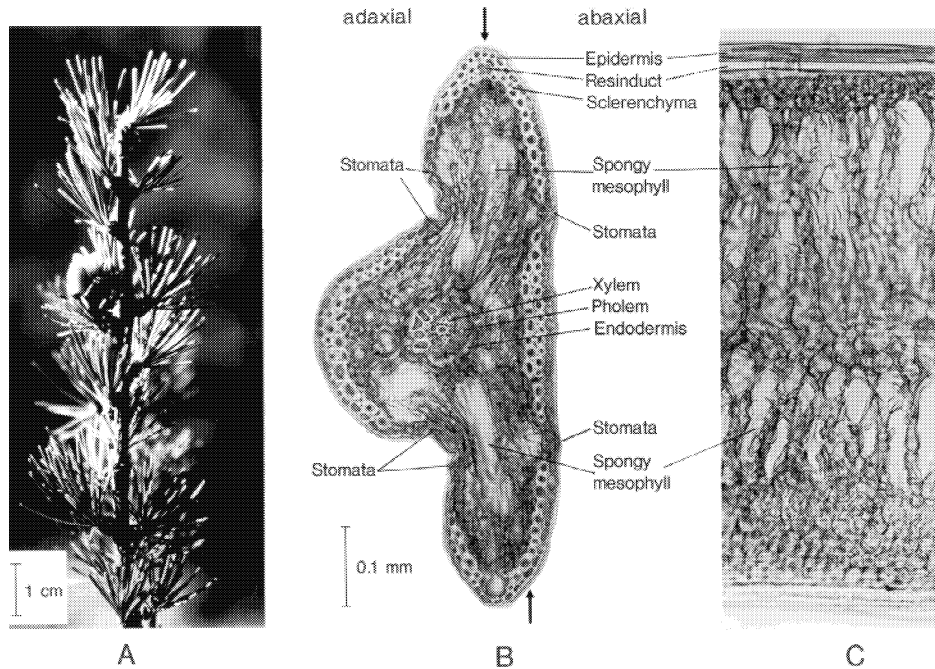


Figure 1A. *Larix gmelinii* needles on a 1-year-old shoot; the needles grow on short-shoots in bundles of 15 to 30 needles. B. Cross-section of a needle. Xylem and phloem are surrounded by a needle endodermis. The assimilatory tissue is supplied with CO₂ from two rows of stomata on the adaxial side and two double rows of stomata on the abaxial-side of the erect growing needle of a short shoot. A longitudinal section was cut through the needle as marked by an arrow on Figure 1B. C: Longitudinal section through the spongy mesophyll. The resin duct at the needle edge is visible.

(92 g m⁻²) and highest values in the sun (187 g m⁻²). The pattern in the crown is complicated because shade-type needles are produced at the basal end of twigs even in the sun-crown.

Needle nitrogen concentration (measured by C/N analyzer, Carlo Erba, Milano, Italy) had a mean of 15.6 ± 0.1 mg g⁻¹ (n = 82) and varied between 11.5 and 16.9 mg g⁻¹ as a result of variation between trees rather than within a tree crown. Leaf nitrogen concentration was not significantly related to leaf

weight per area. Needle N concentration was lower than in *Larix decidua* (24.7 mg g⁻¹, Matyssek and Schulze 1987), but similar to that of the evergreen *Picea abies* (L.) Karst. (14.4 mg g⁻¹, Oren et al. 1988) growing in Central Europe, suggesting that the eastern Siberian deciduous forest is nitrogen limited (Schulze et al. 1995).

Figure 2 shows the daily course of gas exchange of four trees on a typical cloudless Siberian summer day. Air temperatures increased from 15 °C in the morning to 35 °C in the early

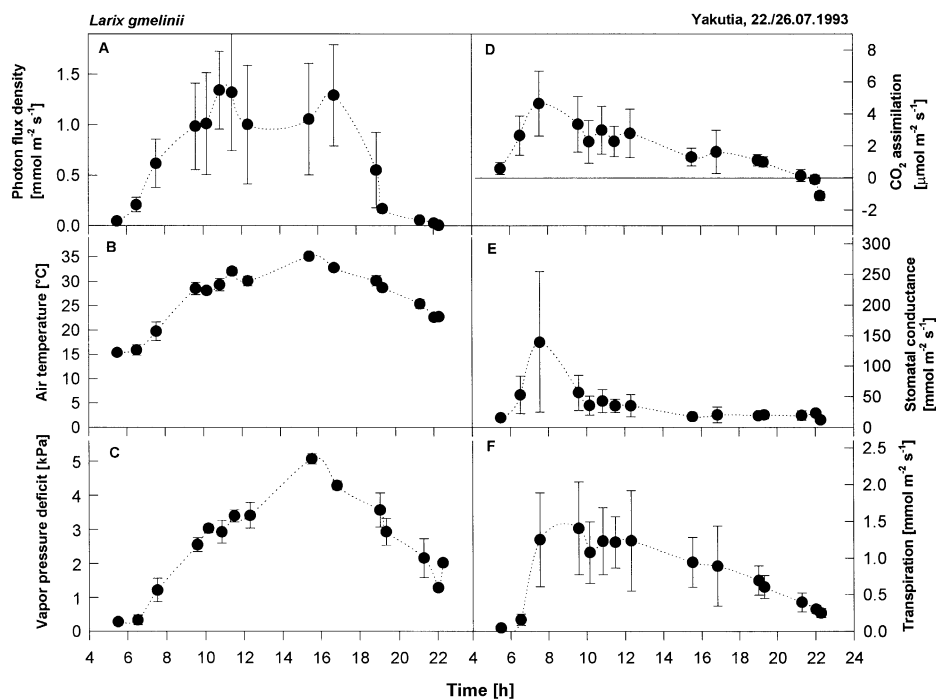


Figure 2. Daily course of gas exchange in *Larix gmelinii* on two clear summer days. The data points represent means and standard deviations (n = 10) of the variation within the crown and between crowns of four trees. A: Photon flux density, B: air temperature, C: vapor pressure deficit, D: CO₂ assimilation, E: leaf conductance, and F: transpiration.

afternoon. Assimilation reached a maximum in the early morning when temperature, light and VPD were still low and then decreased continuously until evening. The decrease in CO₂ assimilation was associated with stomatal closure. Leaf conductance exhibited an early morning maximum and then decreased sharply when VPD increased above 1.0 kPa. Stomatal closure overcompensated for the effect of increased VPD on transpiration, which decreased in parallel with stomatal closure even before noon and despite further increases in VPD.

We defined maximum rates of gas exchange as the mean of the 10 highest single measurements, whereas mean rates included all of the data obtained during the 16-h photoperiod when net assimilation was higher than respiration (Table 2). Mean rates of gas exchange were only about 25% of maximum rates, a proportion that is more typical for plants in arid climates than for plants in temperate climates (Schulze and Hall 1982). Integrating the daily course of gas exchange, and assuming an LAI of 1.4, the porometer data suggest a daytime carbon gain of 0.217 mol m_{soil}⁻² day⁻¹ at a transpirational water loss of 1.45 mm day⁻¹. Estimated daily transpiration was the same as that calculated from the energy balance and soil evaporation (Armeth et al. 1996), but lower than the value of daily transpiration measured by xylem flux, and higher than the value measured by eddy covariance. The CO₂ fluxes measured by eddy covariance (including soil respiration) were lower than the estimate from porometer measurements. Although the techniques yielded different rates, the differences were quite small given that the canopy has a high aerodynamic roughness.

To explore the effects of climate on gas exchange, diurnal gas exchange rates were plotted as a function of light, temperature and VPD. Because the data included not only the variation in weather but also the variation between twigs within the same

Table 2. Summary of maximum (mean of 10 highest data points) and mean rates (mean ± SD) of gas exchange of *Larix gmelinii* and *Vaccinium* spp. between 0600 and 2200 h for the 14-day period between July 14 and 27, 1993, but excluding two days of rain. Eddy correlation fluxes were calculated according to Hollinger et al. 1996. Xylem flux data are from Armeth et al. 1996.

	CO ₂ assimilation (μmol m ⁻² s ⁻¹)	Leaf conductance (mmol m ⁻² s ⁻¹)	Transpiration (mmol m ⁻² s ⁻¹)
Maximum values for <i>Larix</i>	10.1	365	3.9
Mean values for <i>Larix</i>	2.7 ± 2.2	56 ± 60	1.0 ± 0.8
Mean values for <i>Vaccinium</i>	4.7 ± 2.8	50 ± 29	5.0 ± 2.3
Measurement technique	Mean daily canopy gas exchange (mol m _{soil} ⁻² day ⁻¹)		(mm day ⁻¹)
Porometer (14 days)	0.217		1.45
Xylem flux (6 days)			2.10 (10 trees)
Energy balance (6 days)			1.45
Eddy correlation (5 days)	0.165 (6–22 h)		0.94 (canopy)

tree crown and between trees, we used envelope functions to encompass the upper range of measured data (Figure 3) (Watts et al. 1976). Saturation of CO₂ uptake was reached at an irradiance of about 500 μmol m⁻² s⁻¹ (Figure 3A), whereas both conductance and transpiration were light saturated below 200 μmol m⁻² s⁻¹ (Figures 3B and 3C). Rates of assimilation and transpiration decreased at saturating irradiances at VPD > 2.0 kPa. However, at light saturation and VPD < 2.0 kPa, assimilation ranged between 1 and 12 μmol m⁻² s⁻¹, indicating that climate did not account for all of the variation (Figure 3A). As shown below, this variation was caused by the natural variability of needle physiology within the crown of the same tree and between trees.

Assimilation increased with increasing VPD up to 1.5 kPa as a result of the correlated occurrence of low light and high air humidity in the field, but assimilation decreased with fur-

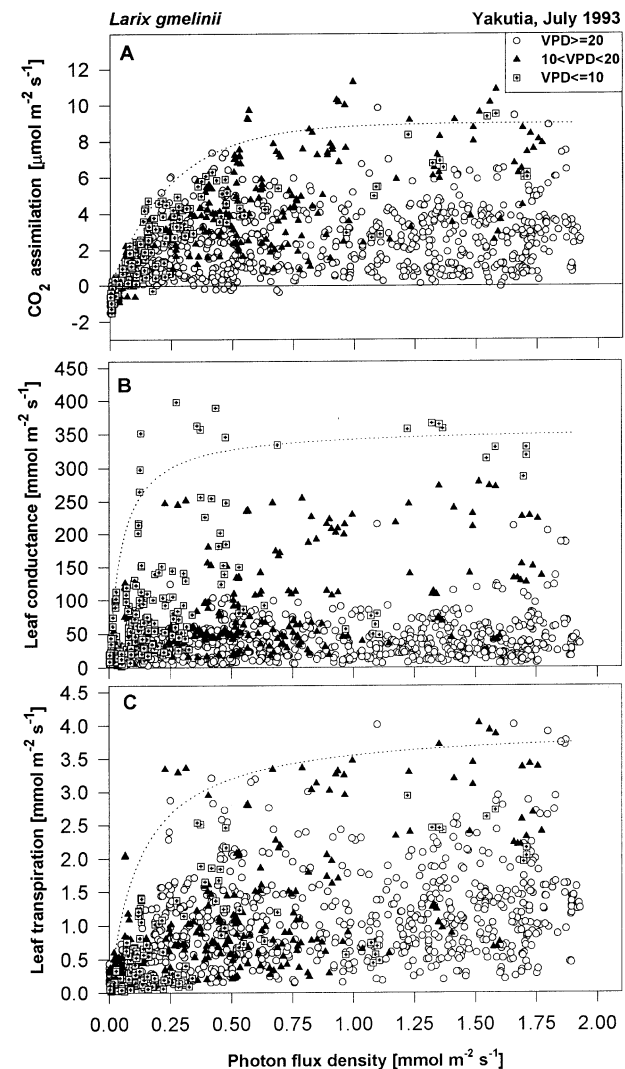


Figure 3. Effects of photon flux density on CO₂ assimilation (A), leaf conductance (B), and transpiration (C). The plots contain observed variation within and between tree crowns ($n = 1200$). The dotted lines represent the following envelope functions: A: $y = 9(1 - e^{-0.004x})$; B: $y = 360x/(x + 50)$; and C: $y = 4x/(x + 125)$.

ther increases in VPD and reached values close to zero at maximum vapor pressure deficits (Figure 4). As VPD increased from 0.5 to 2.5 kPa, leaf conductance decreased 80% to a value of 10–20 mmol m⁻² s⁻¹ at VPD > 2.5 kPa. This value may represent unregulated cuticular conductance, resulting from water loss from damaged stomata or from gradients of VPD within the needle fascicle. Transpiration increased in the morning with increasing VPD and irradiance (Figure 4C), but decreased at VPD > 2.0 kPa as a result of stomatal closure.

It is not clear if the response of leaf conductance to increasing VPD represented a simple humidity response (Lange et al. 1971), because the stomata did not recover in the afternoon when VPD decreased (cf. Schulze et al. 1972). The lack of

stomatal opening in the afternoon was partly because light became limiting; however, at the same irradiance and VPD, more stomata were closed in the afternoon than in the morning. This hysteresis during the course of a dry day may be associated with plant water stress (Schulze 1994), even though transpiration decreased with increasing VPD. No measurements of abscisic acid or plant water status were made.

Plots of assimilation rate and leaf conductance versus air temperature (Figures 5A to 5C) indicated that maximum assimilation rates were reached between 20 and 25 °C and conductance reached maximum values at 20 °C, whereas transpiration reached highest rates between 25 and 30 °C. Because low temperatures occurred only in combination with low irra-

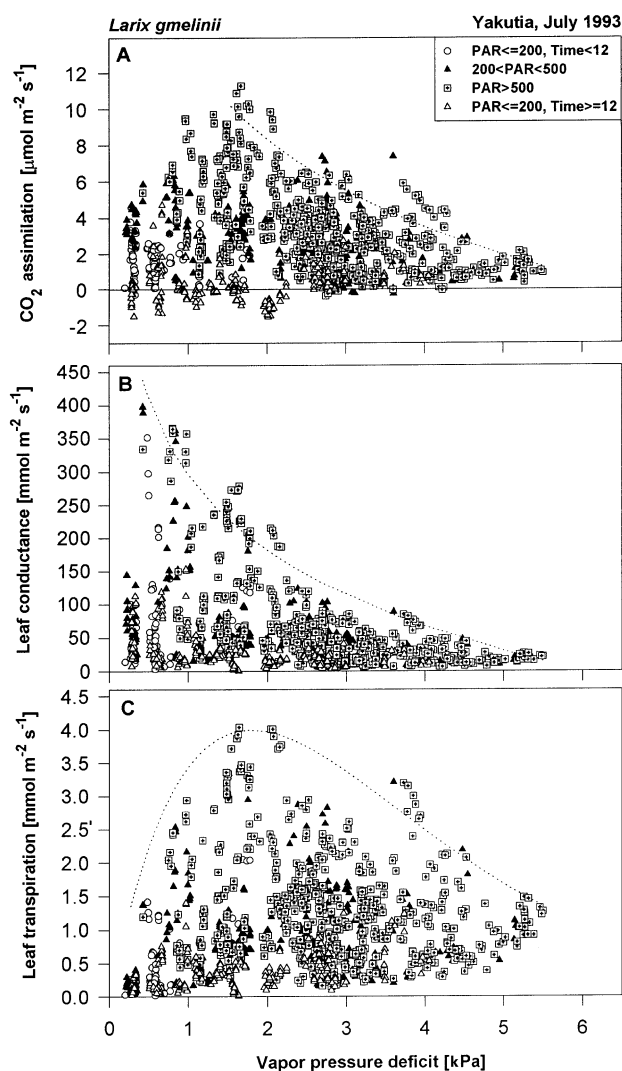


Figure 4. Effect of vapor pressure deficit on CO₂ assimilation (A), leaf conductance (B), and transpiration (C). The plots contain observed variation within and between tree crowns ($n = 1200$). The dotted lines represent the following envelope functions: A: $y = -6.98 \ln(10x) + 29.24$ (the function $y = y_{\max}(1 + \text{VPD}/\text{VPD}_0)$ of Leuning (1995) over-estimates g at high VPD); B: $y = -164.7 \ln(10x) + 675.23$; and C: $y = a(x - x_{\min})(x_{\max} - x)^b$, where $a = y_{\max}/((x_{\text{opt}} - x_{\min})(x_{\max} - x_{\text{opt}})^b)$, and, with $y_{\max} = 4$, $x_{\min} = 0$, $x_{\text{opt}} = 1.8$, and $x_{\max} = 30$.

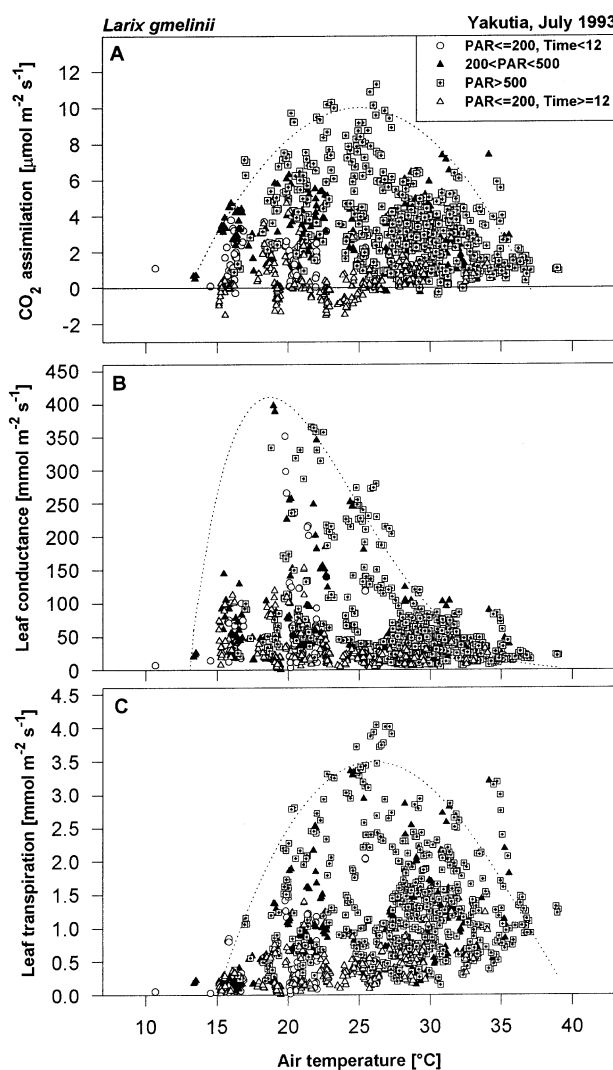


Figure 5. Effect of air temperature on CO₂ assimilation (A), leaf conductance (B), and transpiration (C). The plots contain observed variation within and between tree crowns ($n = 1200$). The dotted lines represent envelope functions of the type $y = a(x - x_{\min})(x_{\max} - x)^b$, where $a = y_{\max}/((x_{\text{opt}} - x_{\min})(x_{\max} - x_{\text{opt}})^b)$, and $b = (x_{\max} - x_{\text{opt}})/(x_{\text{opt}} - x_{\min})$. Parameters: y_{\max} , x_{\min} , x_{opt} , x_{\max} are: A = 10, 13, 25, and 37; B = 350, 13, 22, and 45; and C = 3.5, 15, 26, and 40.

diance under these field conditions, it was not possible to determine whether the physiological optimum of gas exchange was at a lower temperature.

For CO₂-assimilation rates that were not limited by climate, the maximum variation between the different measurements was 7.5 μmol m⁻² s⁻¹, which was 86% of the highest measured rate of CO₂ uptake (Table 3). For conductance, the maximum variation among the measurements was 287 mmol m⁻² s⁻¹, which was 83% of the highest value of leaf conductance. The variation within an exposed branch in the sun-crown (Table 3, case 1) was as large as the variation among branches at the same crown level (Table 3, case 2) or between branches in the sun and shade crown (Table 3, case 3). The variation increased when different trees were considered (Table 3, case 4). It is this variation which makes the use of envelope functions to model assimilation and conductance debatable (Watts et al. 1976), and this limitation is exemplified even more clearly by the humidity response of stomata. In Figure 6, the dotted lines connect consecutive data points taken for each sample during the course of the measuring days. All samples followed the same pattern, namely an increase in conductance with increasing irradiance at low VPD, a very fast (almost linear) stomatal response with increasing VPD at saturating light, reaching a constant low value at about 2.7 kPa, and a hysteresis in the afternoon, when stomata do not open despite decreasing VPD and irradiance. The response of a single twig is denoted by dots. The Lohammer equation ($g = 400/(1 - VPD/1.5)$, Leuning, 1995) explained 75% of the variation of this response, but it underestimated conductance in the VPD range between 1.0 and 2.0 kPa. The main cause for the variation in the response curves of Figure 6 is the capacity of different short shoots for maximum stomatal opening. Each shoot shows the same response type but at a different magnitude of conductance, indicating either that an average curve through the cloud of data points rather than an envelope function best describes the behavior of the canopy with respect to variation in climate, or that response curves must be scaled with respect to maximum performance.

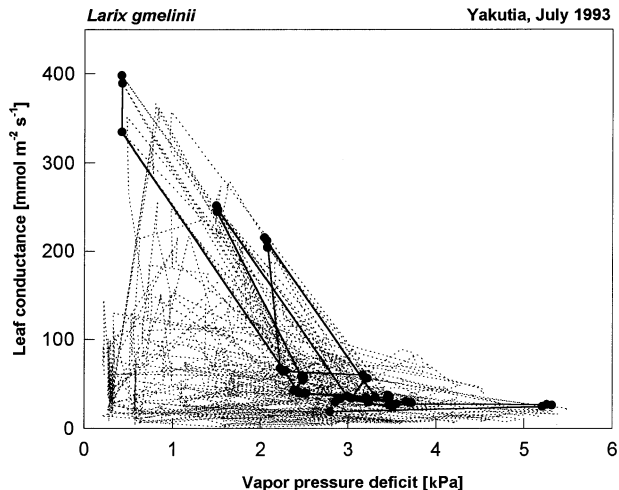


Figure 6. Leaf conductance as a function of vapor pressure deficit in different twigs. Dotted lines connect consecutive measurements during the course of a measuring day. The dots indicate the response of one sample twig on two days. Following Leuning (1995), the response of this twig can be described by $g = 400/(1 + VPD/1.5)$ ($r^2 = 0.75$).

To quantify the combined effects of climate and canopy structure on gas exchange parameters, we investigated the relationships between assimilation and leaf conductance and between assimilation and transpiration (Figure 7). Assimilation increased with conductance initially but then reached a plateau, whereas conductance increased without further increases in CO₂ uptake (Figure 7A). Assimilation was linearly related to transpiration (Figure 7B). The variation in Figure 7 cannot be explained by differences in the sun- and shade-crown, but is inherent to each branch in *Larix*. The mean values of assimilation and conductance correspond to a calculated mesophyll internal CO₂ concentration (p_i) of 241 ppm at an ambient atmospheric CO₂ concentration (p_a) of 340 ppm ($p_i/p_a = 0.71$, according to Field et al. 1989).

Because we do not know the source of the variation causing changes in the physiological performance of short shoots even

Table 3. Variation in maximum values of assimilation and conductance and mean values (mean ± SD) measured on 15 branches from five sample trees and on three twigs along a subsample of each of four branches. The highest and lowest values were selected for different trees, branches and twigs for otherwise optimum climatic conditions.

	Range of assimilation (μmol m ⁻² s ⁻¹)			Range of conductance (mmol m ⁻² s ⁻¹)		
	Minimum	Mean SD	Maximum	Minimum	Mean SD	Maximum
Variation within a branch (1st- to 4th-order twig)	3.6	4.9 ± 2.5	7.5	65	116 ± 79	114
Variation between branches (sun-crown, same tree)	5.4	5.6 ± 2.8	7.4	115	164 ± 119	188
Variation within crown (sun versus shade)	1.2	4.8 ± 2.1	6.0	58	119 ± 84	126
Variation between trees (five neighboring trees)	4.5	5.0 ± 2.5	8.7	151	129 ± 99	345
Maximum range			7.5			287

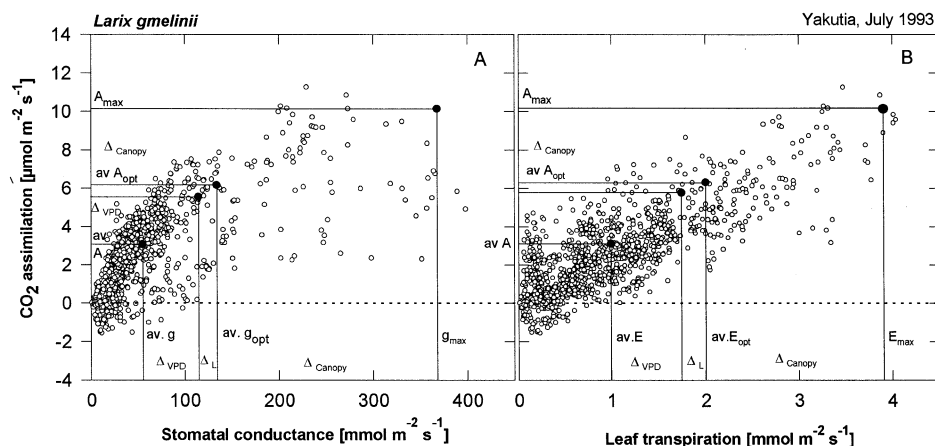


Figure 7. Relationships between CO₂ assimilation and leaf conductance (A) and transpiration (B). The data points represent the variation observed within and between tree crowns ($n = 1200$). Figures 5A and 5B also show the maximum values of gas exchange and leaf conductance as defined by the mean of the 10 highest measured data points, as well as the mean values for gas exchange and leaf conductance measured under non-limiting climatic conditions (light $> 0.5 \text{ mmol m}^{-2} \text{ s}^{-1}$, VPD 1.0 to 1.5 kPa). The difference between the maximum value and the mean value was related to tree structure and variation between trees (Δ_{canopy}). The difference between the mean value measured under climatically non-limiting conditions ($\text{av.}A_{\text{opt}}$, G_{opt} , E_{opt}) and the mean value measured under natural conditions ($\text{av.}A$, G , E) was caused by unfavorable irradiance (Δ_L) and VPD (Δ_{VPD}).

along a single branch, we cannot run a mechanistic model to quantify the effects of canopy parameters and climate on gas exchange. However, we can quantify these effects based on the maximum rate of gas exchange, defined by the 10 highest data points for each parameter (Figure 7 and see Table 2). Maximum values were reduced by effects of canopy parameters and by adverse climatic conditions, resulting in the mean daily values shown in Figure 7 ($\text{av.}g$, $\text{av.}A$, and $\text{av.}E$). The effect of canopy parameters, Δ_{canopy} , was estimated as the difference between maximum values (10 highest values) and mean values of all gas exchange measurements under non-limiting climatic conditions (Figure 7, $\text{av.}g_{\text{non-1}}$, $A_{\text{non-1}}$, $E_{\text{non-1}}$). The total effect of climate is represented by the difference between gas exchange under non-limiting conditions and the mean rates of the total daily course. This difference was separated into effects of light, Δ_L , and VPD, Δ_{VPD} , according to the duration of these non-limiting conditions in the natural climate and the corresponding gas exchange value (mean assimilation at non-saturating light for 2 h and mean assimilation at VPD < 2.0 kPa for 12 h as a percentage of mean assimilation during 14 h of non-optimal climate). The mean values under non-limiting climatic conditions were about 39% lower than the maximum rate of assimilation and 64% lower than maximum conductance. This is a large structure-dependent variation in gas exchange for an open canopy. Low irradiance decreased the maximum values of assimilation and conductance by 6%, whereas VPD reduced assimilation by 26% and conductance by 16%. Similar observations were made for canopy and climate effects on transpiration.

Discussion

Maximum rates of assimilation of needles reached about $10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ in *Larix gmelinii*, which was three times

higher than maximum rates of its close relative, *L. decidua*, growing in temperate Europe (Benecke et al. 1981) and higher than in Japanese *Larix leptolepis* (Siebold & Zucc.) Gord. and the North American *Larix laricina* (Du Roi) C. Koch. (Matyssek and Schulze 1987, Dang et al. 1991). The high maximum assimilation rate of *Larix gmelinii* was associated with higher conductances, and much higher transpiration rates compared with other *Larix* species. In *Larix decidua*, transpiration rates reached $0.75 \text{ mmol m}^{-2} \text{ s}^{-1}$ when VPD was 1.5 kPa, which is only 20% of the maximum water loss in *L. gmelinii* at the same VPD. These rates are high given that the mean nitrogen concentration of *L. gmelinii* needles (mixed sample of a tree crown) was only 60% of European larch needles. However, the needle cross section indicated that a large fraction of the needle dry weight was associated with sclerenchyma cells; hence, nitrogen per leaf area was only 20% lower than in European larch. In ecological terms, the high maximum rate of assimilation of *L. gmelinii* is essential because of the short summer in a continental climate. Even on a daily basis, climatic conditions for maximum assimilation are very short. In July, only 2 out of 16 h (12% of daytime) would support maximum rates. Thus, this species is under strong selective pressure to assimilate rapidly whenever conditions are favorable, not only on a yearly basis but also on a daily basis. This is achieved by needles concentrating N in a spongy mesophyll. The thick sclerenchyma may serve to maintain structural integrity of the needle when water stress develops. The mesophyll cells are not densely packed and can perform large turgor changes without causing mechanical damage to the parenchyma.

The large variation in gas exchange within and between branches most probably results from internal reallocation of nitrogen as has been described for herbaceous and woody species (Field 1983, Givnish 1986, Stitt and Schulze 1994).

This reallocation is most likely responsible for the large structural variation in assimilation within a crown and between trees. Variations in maximum and minimum needle N concentrations were about 40% on average. Thus, the cost of high photosynthetic capacity in some parts of the crown, is a large variation within a crown. More data on the effects of canopy architecture on nitrogen distribution are needed to demonstrate unequivocally that the large within-crown variation results in a higher assimilation for the canopy as a whole.

The response of gas exchange to environmental conditions was similar to that of other *Larix* species. *Larix decidua* opened stomata at low light and reached light saturation at about $500 \mu\text{mol m}^{-2} \text{s}^{-1}$. In *L. decidua*, conductance decreased at $25 \text{ mmol m}^{-2} \text{s}^{-1}$ per kPa (Benecke et al. 1981, Sandford and Jarvis 1986, Matyssek and Schulze 1987), and this was similar to *L. gmelinii*, which closed stomata at a mean rate of $30 \text{ mmol m}^{-2} \text{s}^{-1}$ per kPa, and stomata closed over about the same range of VPDs in both species. In contrast to the European larches, however, transpiration only decreased in the dry air of Siberia, mainly because VPD never reached such high values in Europe. We obtained no evidence of a major adaptive response in the regulation of gas exchange by climate in *L. gmelinii*. However, under the extreme climatic conditions of eastern Siberia, the reductions in maximum assimilation rate as a result of low irradiance (12% reduction) and low air humidity (75% reduction) were similar to those observed for fruit trees (*Prunus armeniaca* L.) in arid agriculture systems (Schulze and Hall 1982), where maximum assimilation was reduced 15% by low irradiance and 63% by low air humidity.

The existence of *Larix gmelinii* in this continental climate depends on water supply from thawing permafrost in summer (Kelliher et al. 1997). Because temperatures reach freezing point at about 0.7 m soil depth in summer, it is expected that water uptake is temperature limited. During the day, water stored in the stem and taken from soil surrounding the root is most likely consumed in the morning. The supply of water may become limiting during some afternoons and in combination with dry air, it may determine the response of stomata. The lack of recovery of stomata is an indication of water stress (Schulze 1994).

We quantified the response of *Larix gmelinii* and compared it with other species by examining the daily carbon gain in relation to needle carbon investment. Oren et al. (1986) postulated a linear relationship between daily carbon gain and leaf mass per area (g m^{-2}). *Larix decidua* reached about $175 \text{ mmol CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ at $130 \text{ g m}_{\text{leaf}}^{-2}$, whereas *L. gmelinii* reached about $220 \text{ mmol CO}_2 \text{ m}^{-2} \text{ day}^{-1}$ at the same needle weight per area despite the much harsher atmospheric conditions in Siberia than in Central Europe. We conclude that the efficient investment of the nitrogen-limiting resource into photosynthetic machinery contributes to the dominance of this species in the Siberian boreal desert.

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