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The Effects of Environmental Variables on Gas Exchange of Several Tree Species Under Boreal Field Conditions*

环境变化对几个树种在北方田间条件下气体交换的影响

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Abstract The influence of environmental conditions on gas exchange of aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), hazelnut (*Corylus cornuta* Marsh.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill) BSP) was examined during the summers of 1994 and 1995 in the boreal forest near Prince Albert, Saskatchewan, Canada. Gas exchange rates were measured with a portable gas exchange system. The results showed that there were significant effects of photosynthetic photon flux density (*PPFD*), air temperature (*Ta*), vapor pressure deficit (*VPD*) and internal CO_2 concentration (*Ci*) on gas exchange. The effects differed among the different species. Under ambient CO_2 concentrations (*Ca*), and relatively constant *Ta* and *VPD*, aspen showed a higher light saturation point, quantum yield of assimilation (H), and maximum assimilation at saturating *PPFD* (*Pm*), and a lower light compensation point (*LCP*) than either jack pine or black spruce. In aspen, the photosynthetic capacity was higher in younger trees than in older trees, and was higher in the earlier growing season than in the later growing season. Stomatal conductance (*gs*) increased with increasing *PPFD* for both aspen and jack pine. There was no obvious effect of *PPFD* on *gs* for black spruce. Under high light ($PPFD > 1\,000 \mu mol\ m^{-2}\ s^{-1}$), young aspen leaves from shaded canopy positions showed lower net CO_2 assimilation (*A*), *gs* and dark respiration (*Rd*) than sun leaves from exposed canopy positions. There were no statistical differences in *Pm*, H and *Rd* between jack pine and black spruce. Under high light, as *Ta* increased from 15℃ to 35℃, *A* and *gs* increased for aspen, decreased for black spruce and were not obviously influenced for jack pine. Net assimilation rate and *gs* were highest in the *Ta* range of 24℃～29℃ for aspen, 22℃～28℃ for jack pine and 21℃～27℃ for black spruce. The effect of *VPD* on gas exchange was significant for aspen, jack pine and black spruce which showed that *A* and *gs* increased with decreasing *VPD*. The current-year shoots usually showed lower *A* than those of 1- and 2-year old shoots for jack pine and black spruce. There was no difference in gas exchange between 1- and 2-year old shoots in either conifer species. The initial slopes of the *A-Ci* responses (i.e., carboxylation efficiency (*CE*)) were *PPFD*-dependent and differed among species and tree ages. In general, *CE* followed the pattern: aspen> balsam poplar> hazelnut> jack pine, and young aspen> old aspen. The overall results indicated that light was the major determinant of photosynthetic rate, although the rate was modified by *Ci*, *Ta* and *VPD*. Under high light, the major environmental influences on gas exchange were *Ta* and *VPD*.

Key words tree species, gas exchange, net CO_2 assimilation, stomatal conductance, photosynthesis, photosynthetic photon flux density, air temperature, vapor pressure deficit

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摘要　1994年和 1995年夏季在加拿大 Saskatchewan省 Prince Albert市北部森林测定环境条件对欧洲杨(*Populus tremuloides* Michx.),胶杨(*Populus balsamifera* L.),榛子(*Corylus cornuta* Marsh.),短叶松(*Pinus banksiana* Lamb.)和黑云杉(*Picea mariana* (Mill) BSP)气体交换的影响。气体交换率的测定使用便携式气体交换系统(LI-6200)。结果表明光合作用光流动量(*PPFD*)、气温(*Ta*)、蒸气压差(*VPD*)和体内二氧化碳浓度(*Ci*)均对气体交换有显著影响,但对不同树种影响程度不同。在大气二氧化碳浓度(*Ca*)和相对稳定的气温和蒸气压差下,欧洲杨比短叶松和黑云杉有较高光饱和点、同化量子产量(H)、在饱和 *PPFD*下最高同化率(*Pm*)和较低的光补偿点(*LCP*)。对欧洲杨树,幼龄树比老龄树有较高光合能力,且生长季早期光合能力比后期高。欧洲杨和短叶松的气孔导度(*gs*)随 *PPFD*增加而增加。但黑云杉 *gs*不受 *PPFD*影响。在高光强下($PPFD > 1\,000$ $\mu mol\cdot m^{-2}s^{-1}$),欧洲杨幼树被光叶片比曝光叶片表现较低的净二氧化碳同化率(*A*)、*gs*和暗呼吸(*Rd*)。短叶松和黑云杉 *Pm*、H和 *Rd*没有统计上差异。在高光强下,当气温从 15℃增至 35℃时,欧洲杨 *A*和 *gs*增加,黑云杉的降低,而短叶松没有明显变化。欧洲杨 *A*和 *gs*最高值的适宜的气温是 24℃～29℃,短叶松是 22℃～28℃,黑云杉是 21℃～27℃。*VPD*明显影响欧洲杨、短叶松和黑云杉的气体交换,*A*和 *gs*均随 *VPD*降低而增高。短叶松和黑云杉当年生树枝 *A*通常比一年龄和二年龄树枝低。两个针叶树种一年龄和二年龄树枝的气体交换没有明显差异。*A*-*Ci*反应的斜率(即羧化效率(*CE*))取决于 *PPFD*、树种和树龄。一般情况下,*CE*遵循以下模式:欧洲杨 > 胶杨 > 榛子 > 短叶松,欧洲杨幼树 > 老树。总的结果表明尽管 *Ci*、*Ta*和 *VPD*改变光合作用效率,但光是最主要的因子。在高光强下,影响气体交换的环境因子是气温和蒸气压差。

关键词　树种　气体交换　净二氧化碳同化率　气孔导度　光合作用　光流动量　气温　蒸气压差
中图法分类号　S 792.110.1; S 791.242.01

Plant growth and primary ecosystem productivity are ultimately dependent on photosynthesis. Many previous studies have found that leaf gas exchange are influenced by many interrelated factors, both environmental and physiological including photosysthetic photon flux density (*PPFD*), air temperature (*Ta*), atmospheric CO_2 concentration (*Ca*), vapor pressure deficit between plant leaf and air (*VPD*), soil moisture, plant nutrition and foliage age.[1-3] The quantification of these influences and the ability to accurately predict gas exchange as a function of environmental conditions is useful in many endeavors.[4]

Aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill) BSP) are the principal woody species of the North American boreal forest.[5,6,3] Jack pine is typically found at drier sites than black spruce while aspen occurs in moderately moist sites.[7,8] Relatively little is known about gas exchange responses of boreal tree species to environmental conditions and most studies have focused on seedlings.[9] Dang et al.[10] investigated gas exchange of 20-year-old black spruce and concluded that *Ta* is an important environmental factor limiting tree growth. Increased knowledge about the gas exchange response of these species to environmental factors is very important for understanding limitations to productivity in these species and for assessing the impact of climatic change on the boreal forest. In this regard, studies of gas exchange in the field are often more useful than those conducted in the nursery or greenhouse, and those with mature trees are more useful than those with seedlings.[11]

The objective in this study was to quantify the influence of *PPFD*, *Ta*, *VPD*, and CO_2 concentration on *A* and stomatal conductance (*gs*) of aspen, jack pine and black spruce under field conditions in the boreal forest.

1 Materials and methods

1.1 Study sites

The study was conducted in the BOREAS (Boreal Ecosystem Atmosphere Study) Southern Study Area (SSA) at four sites near Prince Albert, Saskatchewan, Canada during the summers of 1994 and 1995. Five woody species were selected for the experiment: aspen, hazelnut (*Corylus cornuta* Marsh.), balsam poplar (*Populus balsamifera* L.), jack pine and black spruce. Aspen trees, 50～100 years old (old aspen) with heights of 15 m～20 m, were located on well drained soils at the SSA mixed site (SSA-MS, 5 km southeastern Candle Lake, Saskatchewan). Aspen trees, 14～24 years of age (young aspen), with heights of 5 m～8 m, were growing with hazelnut and balsam poplar at the SSA young aspen site (SSA-YA, 53.709°N, 105.31°W). This site was located in an upland area where the silt loam soils have a high available water holding capacity and are relatively nutrient rich. Jack pine trees, 11～16 years of age with heights of 4 m～6 m, were located at the SSA young jack pine site (SSA-YJP, 53.875°N, 104.65°W). Soil texture is sandy with a 10 cm～15 cm organic layer, characterized by very rapid drainage. Soil drought is common.[12] Black spruce trees, up to 100 years of age, with heights of 11 m～15 m, were located at the SSA old black spruce site (SSA-OBS, 53.985°N, 105.12°W). This site has sandy loam soils with a 5 cm～20 cm organic layer and is located in a lowland area which is wet, cold, nutrient poor and poorly drained.[7]

1.2 Gas exchange measurements

Gas exchange was measured *in situ* on the most recently fully expanded and unshaded leaf blades of old and young aspen, hazelnut and balsam poplar in 1994 and on unshaded shoots of three age classes of jack pine and black spruce in 1994 and 1995. In 1994 the study area was characterized by high *Ta* and high *VPD*.[13] In addition gas exchange measurements of shaded leaves of young aspen located inside the canopy were made under high light conditions. Responses of *A* and *gs* to short-term variations in environmental conditions were determined in the field with a portable gas exchange system (LI-6200 Portable Photosynthesis System, Li-Cor Inc., Lincoln, NE, USA) using a one liter chamber, in the closed circuit mode. Leaves or shoots were sampled randomly within the canopies. Measurements for young aspen, hazelnut, and balsam poplar leaves and jack pine shoots were made at a height below 2 m while those for old aspen leaves and black spruce shoots were made from a 10 m~ 15 m instrument tower scaffold. All needles in jack pine are less than 5 years, while some of the needles in black spruce are more than 10 years. Gas exchange properties for jack pine and black spruce were measured the three youngest age classes on the same branch (hereafter designated as current-, 1- and 2-years growth). *PPFD*, *Ta*, leaf temperature (*Tl*), *VPD* and relative humidity (*RH*) were recorded during the measurements. Stomatal conductance was calculated assuming a boundary layer conductance previously determined with pieces of wet filter paper of a similar size and shape to the leaves (in the case of broadleaf samples) or with a moistened shoot in the measurement chamber (in the case of conifer samples). Net assimilation rate was estimated based on the mean slope of CO_2 depletion in the chamber; internal CO_2 concentration (*Ci*) was calculated from *gs* and *A* values.[14, 15] The relationship between *A* and *Ci* was measured at several *PPFD* levels from 300 μmol m^{-2} s^{-1} to 1 870 μmol m^{-2} s^{-1}. Various *PPFD* levels were obtained by attenuating direct sunlight with one or more neutral density filters over the leaf or shoot. Filters were installed 30 min prior to initiating measurements. Precautions during the measurement period followed the suggestions of McDermitt et al[16]. to maintain relatively stable *Ta* and *VPD* inside the chamber, and to correct for potential leakage from the sample chamber during the entire *A*-*Ci* measurement. The measured leaf or shoot was harvested after completion of gas exchange measurements. Broadleaf area was determined as the area within a tracing of leaf outlines on ruled graph paper. The total needle surface area (*SA*) for conifers was determined using the displaced volume method[17] which involved submerging a shoot in a water-filled container, weighing the sample submerged in the container (*v*), counting the number of needles on the shoot (*n*), and determining an average needle length (*l*) from a random sample of 10 needles. The total needle surface area was calculated as: $SA = \theta \times (vnl)^2$, where θ is the shape factor determined from a random sample of 35 needles. The shape factors for jack pine and black spruce were 4.36 and 4.00, respectively.

1.3 Curve-fitting and parameter calculations

Light and CO_2 response curves were fitted with the monomolecular function via nonlinear regression[18]:

$$A = a \times (1 - \exp^{(b - c \times Ci \text{ or } PPFD)}) \qquad (1)$$

where *a*, *b* and *c* are the fitted coefficients, where *a* represents the maximum rate of *A* at saturated *PPFD* (*Pm*) or saturated *Ci*. The equation can be simplified for conditions at the light compensation point (*LCP*) or CO_2 compensation point (Γ) (i.e., when $A = 0$) so that the ratio b/c is *LCP* or Γ. Likewise equation (1) can be solved for quantum yield of assimilation or photochemical efficiency (Φ) and carboxylation efficiency (*CE*) ($dA/dPPFD$ at $PPFD = 0$ or dA/dCi at $Ci = 0$) as $a \times c \times \exp^{b}$.

1.4 Statistical analysis

Nonlinear and linear regressions were utilized to interpret the relationships between gas exchange and independent variables. In certain instances, gas exchange responses were interpreted with data separated by *PPFD*, *Ta* (or *Tl*) and *VPD* as independent variables. Gas exchange response to *PPFD* for young aspen was analyzed by dividing the data into two distinct groupings based on growing season. Gas exchange responses to *Ta* and *VPD* for aspen, jack pine and black spruce were analyzed by restricting the analysis to samples under high light conditions ($PPFD > 1\ 000$ μmol m^{-2} s^{-1}). Analyses of variance were performed to assess the differences in response among different conditions and species. All analyses were performed using StatView[19] and SAS.[20] Effects were considered statistically significant when the probability of Type I error was 0.05 or less.

2 Results and discussion

2.1 Response of gas exchange to *PPFD*

The light response curves for all species were of the same form but values of *A* differed significantly among aspen, jack pine and black spruce (Fig. 1), although the *Tl* and *VPD* among the three species were similar during the gas exchange measurements (Table 1). Net assimilation rate increased linearly as *PPFD* increased from 50 μmol m^{-2} s^{-1} to 500 μmol m^{-2} s^{-1}, in the conifers, and then reached a clearly defined asymptote. For aspen, the asymptotes were less clearly defined (e.g., the late season aspen data in Fig. 1). Assimilation became relatively independent of *PPFD* when $PPFD >$ ca. 1 000 μmol m^{-2} s^{-1}. Aspen showed

Table 1 Leaf or shoot temperature (*T*1) and vapor pressure deficit (*VPD*) during leaf and shoot gas exchange measurements. Quantum yield of assimilation (Φ), light saturated of net assimilation rate (*Pm*), light compensation point (*LCP*) and dark respiration (*Rd*) were calculated from light response curves showed in Fig. 1.

Species	Age	*Tl* (℃)	*VPD* (kPa)	H	*Pm* (μmol m^{-2} s^{-1})	*LCP* (μmol m^{-2} s^{-1})	*Rd* (μmol m^{-2} s^{-1})
Aspen	young1	23.3 ± 0.3†	1.88 ± 0.05	0.0652	9.62	51.4	2.94
	young2	24.0 ± 0.4	1.64 ± 0.06	0.0510	16.5	42.5	2.05
	old	25.9 ± 0.3	2.07 ± 0.05	0.0564	13.5	41.4	2.17
Jack pine	1995-C	24.8 ± 0.5	1.84 ± 0.07	0.0306	3.85	124.6	2.90
	1995-1	25.4 ± 0.5	1.90 ± 0.07	0.0234	6.00	60.7	1.29
	1995-2	25.2 ± 0.6	1.97 ± 0.09	0.0209	5.25	72.2	1.35
Black spruce	1995-C	23.4 ± 0.4	1.66 ± 0.08	0.0510	3.54	85.1	3.20
	1995-1	24.1 ± 0.4	1.80 ± 0.08	0.0241	4.57	89.8	1.65
	1995-2	25.2 ± 0.3	2.00 ± 0.06	0.0199	4.09	100.3	1.68

† ± standard error of the mean.

a higher light saturated point as compared with jack pine and black spruce (Fig. 1a). Also aspen had higher H and *Pm*, and lower *LCP* as compared with jack pine and black spruce (Table 1). Light response curves for aspen were different between young and old trees and between different times in the growing season for young trees. For aspen, maximum *A* at saturating *PPFD* was lower, and H, *Rd* and *LCP* were higher early in the growing season as compared with late in the growing season. This result is consistent with the seasonal pattern of gas exchange (observed by us). When compared with old trees during the same measuring period (*DOY* 172–219), young aspen showed higher *Pm* (16.5 μmol m^{-2} s^{-1} for young aspen verses 13.5 μmol m^{-2} s^{-1} for old aspen, Fig. 1a and Table 1). Kull and Koppel[21] showed that maximum photosynthetic capacity of Scots pine (*Pinus sylvestris*) declined as trees aged. Yoder et al.[22] reported that net photosynthesis per unit area of 1-year-old foliage from old *Pinus contorta* and *Pinus ponderosa* averaged 14% ~ 30% lower than the same-aged foliage from younger trees. They suggested that a possible reason for lower photosynthesis rates in older trees might be lower hydraulic conductance in the vascular systems leading to greater stomatal closure. However, Sullivan et al.[23] reported that *gs* limitation to *A* did not vary between the young and old stands of jack pine. In our study, the results indicated that different *A* between species, tree age and growing season may correlate with *gs*. Differences in light response curves were observed between current-year and 1-and 2-year old shoots of jack pine (Fig. 1b). The current-year shoots had a lower *Pm*, higher *LCP* and *Rd* when the needles were expanding. There were no differences between 1- and 2-year old shoots for jack pine. Similar results were observed for jack pine as part of BOREAS.[23] The current-year shoots of black spruce had fully developed when measurements were made and no differences in light response curves were observed among shoots representing the three age classes (Fig. 1c).

Stomatal conductance increased linearly with increasing *PPFD* for all three species except for the current- and 1-year old shoots of black spruce (Fig. 2). Differences in *gs* were observed between aspen and both conifers and coincided with results of *A*-*PPFD* curves. Aspen showed significantly higher *gs* than jack pine or black spruce. The means of *gs* were 0.222, 0.072, and 0.085 μmol m^{-2} s^{-1} for aspen, jack pine and black spruce, respectively (Fig. 2). The effect of *PPFD* on *gs* for aspen was significant (Fig. 2a). The slope and intercept of *gs* were significantly higher in young trees than in old trees for aspen, and in the late growing season than in the early growing season for young aspen. These differences might relate to their physiological process. Kloeppel et al.[24] reported that fully expanded foliage sampled for four successional Pennsylvania barrens species at the beginning of the growing season may not have reached their full morphological or physiological potential for maximum gas exchange values. Though the current-year shoots had lower *Pm* and higher *Rd*, jack pine showed higher *gs* than those in the 1- and 2-year old shoots (Fig. 2b). Teskey et al.[25] reported that the content of waxes on the needle surface in *Abies amabilis* increased with increasing age. Thus, high *gs* in the current-year shoots might result from relatively higher cuticular conductances due to less wax on the needle surfaces. There was no obvious relationship between *PPFD* and *gs* in the current- and 1-year old shoots of black spruce. Though the effect of *PPFD* on *gs* was obvious in the 2-year old shoots there was no statistical difference among the three age classes (Fig. 2c). The effect of *PPFD* on *gs* was thus more readily apparent in jack pine than in black spruce. Jack pine is classified as a very shade-intolerant species while black spruce is very shade-tolerant species[26] which may be related to their response of *gs* to *PPFD*.

Differences in gas exchange between sun and shade leaves were observed in young aspen trees (Table 2). Under the same environmental conditions, *A*, *gs* and *Rd* of sun leaves were higher than those of shade leaves. Similar results have been reported in leaves of four *Actinidia sinensis* cultivars[27], *Silphium terebinthinaceum*[28] and needles of *Abies amabilis*[29]. Brooks et al.[29] reported that sun foliage exhibited higher *A* and *Rd* due to higher N content and chlorophyll a: b ratio, and a lower chl: N ratio than shaded foliage.

2.2 Response of gas exchange to *Ta*

The effect of *Ta* on gas exchange was not well defined but appeared to differ among the three species (Fig. 3) under high *PPFD* (> 1 000 μmol m^{-2} s^{-1}), ambient *Ca* (ca. 350 μmol mol^{-1}) and relatively constant *VPD* (2.01 kPa~ 2.36 kPa). Net assimilation rate increased with increasing *Ta* for aspen (Fig. 3a), decreased for black spruce (Fig. 3c), and showed no response to *Ta* for jack pine (Fig. 3b). The optimum ranges of *Ta* also varied between species and was about 24℃~ 29℃ for aspen, 22℃~ 28℃ for jack pine and 21℃~ 27℃ for black spruce. The response of *gs* to *Ta* was similar to that of *A* for the three species (Fig. 4). The different response of the three species to *Ta* was

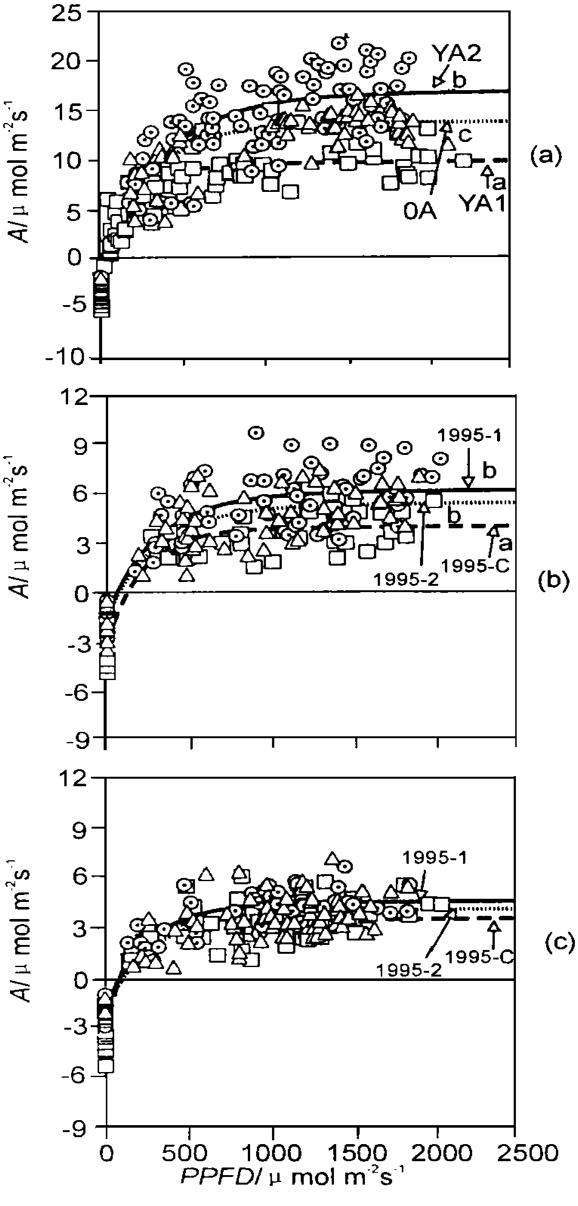

Fig. 1 Net CO_2 assimilation rate (*A*) as a function of photosynthetic photon flux density (*PPFD*) in aspen leaves and jack pine and black spruce shoots. Symbols represent observations of different leaves and shoots and the curves were plotted by fitting the data to Eq[1]. Different letters denote significantly different values at $P < 0.05$. Environmental conditions during measurements are reflected in Table 1. Note difference in scale for this and other figures

(a) Young and old aspen □ YA1, ⊙ YA2, △ OA; (b) Jack pine □ 1995-C, ⊙ 1995-1, △ 1995-2; (c) Black spruce □ 1995-C, ⊙ 1995-1, △ 1995-2

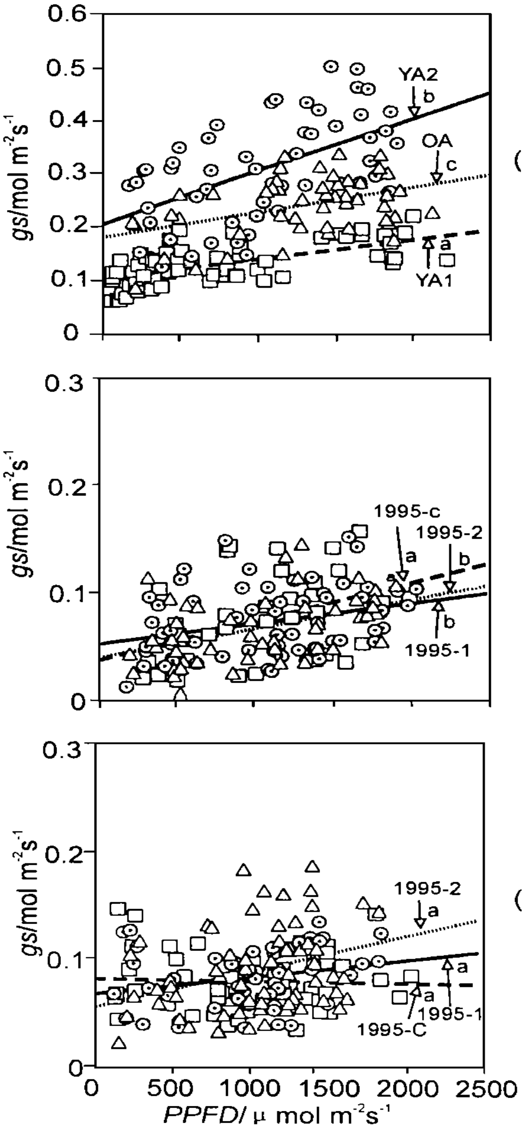

Fig. 2 The response of stomatal conductance (*gs*) to photosynthetic photo flux density (*PPFD*) in aspen leaves and jack pine and black spruce shoots under ambient CO_2 concentration, *Tl* of 23℃~ 26℃ and *VPD* of 1.5~ 2.0 kPa. Symbols represent observations of different leaves and shoots. Different letters denote significantly different values at $P < 0.05$.

(a) Young and old aspen □ YA1, ⊙ YA2, △ OA; (b) Jack pine □ 1995-C, ⊙ 1995-1, △ 1995-2; (c) Black spruce □ 1995-C, ⊙ 1995-1, △ 1995-2 expected as they differ in both genetic potential and site-specific growth conditions.

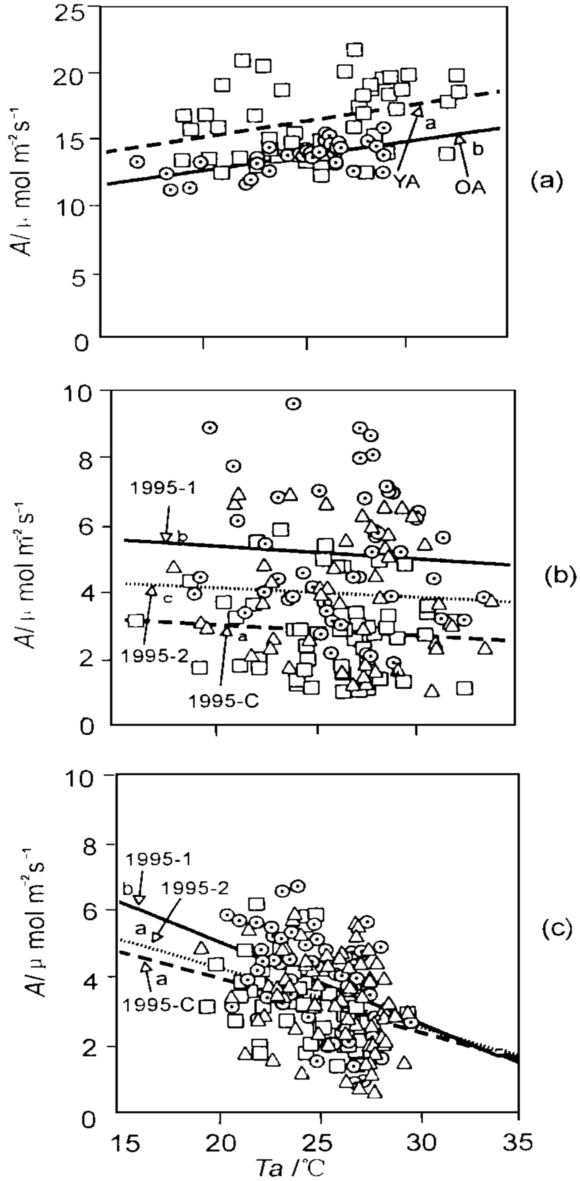

Fig. 3 The response of net CO_2 assimilation rate (A) to air temperature (Ta) in aspen leaves and jack pine and black spruce shoots under $PPFD > 1\ 000\ \mu mol\ m^{-2}\ s^{-1}$, ambient CO_2 concentration, and VPD of 2.0 kPa~ 2.4 kPa. Symbols represent observation of different leaves and shoots. Different letters denote significantly different values at $P < 0.05$

(a) Young and old aspen: □ YA, ⊙ OA; (b) Jack pine: □ 1995-C, ⊙ 1995-1, △ 1995-2; (c) Black spruce: □ 1995-C, ⊙ 1995-1, △ 1995-2

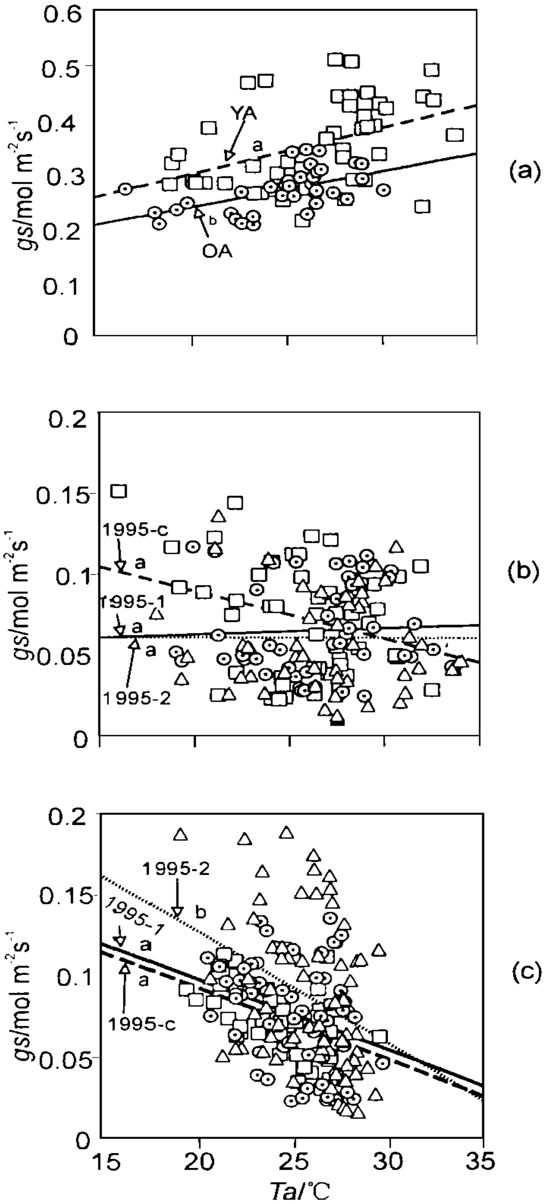

Fig. 4 The response of stomatal conductance (gs) to air temperature (Ta) in aspen leaves and jack pine and black spruce shoots under $PPFD > 1\ 000\ \mu mol\ m^{-2}\ s^{-1}$, ambient CO_2 concentration, and VPD of 2.0 kPa~ 2.4 kPa. Symbols represent observations of different leaves and shoots. Different letters denote significantly different values at $P < 0.05$.

(a) Young and old aspen: □ YA, ⊙ OA; (b) Jack pine: □ 1995-C, ⊙ 1995-1, △ 1995-2; (c) Black spruce: □ 1995-C, ⊙ 1995-1, △ 1995-2

Table 2 Average photosynthetic photon flux density (*PPFD*), leaf temperature(*Tl*), vapor pressure deficit (*VPD*), net assimilation rate (*A*), stomatal conductance (*gs*) and dark respiration (*Rd*) for sun and shade leaves of young aspen at 0930-1430 central standard time (CST) on July 22 and 23 of 1994

Leaf position	$PPFD$ ($\mu mol\ m^{-2}\ s^{-1}$)	Tl (℃)	VPD (kPa)	A ($\mu mol\ m^{-2}\ s^{-1}$)	gs ($mol\ m^{-2}\ s^{-1}$)	Rd ($\mu mol\ m^{-2}\ s^{-1}$)
Sun	1537± 0.13	27.14± 132	2.26± 0.45	$17.16^{a\dagger}$ ± 0.13	0.358^{a}± 0.87	2.48^{a}± 0.019
Shaded	1498± 143	27.27± 0.45	2.38± 0.15	12.14^{b}± 0.92	0.272^{b}± 0.029	1.98^{b}± 0.07

† Followed by different letters within a column are significantly different ($P < 0.05$).

2.3 Response of gas exchange to *VPD*

Net assimilation rate and gs responses to VPD for the three species under high light ($PPFD > 1000\ \mu mol\ m^{-2}\ s^{-1}$) are presented in Figs. 5 and 6. The ranges of VPD were from 1.0 kPa to 3.5 kPa for aspen and black spruce, and 1.0 kPa to 6.0 kPa for jack pine. Effects of VPD on A and gs were observed in leaves of old aspen, and shoots of different ages of jack pine and black spruce. Net assimilation rate and gs decreased linearly with increasing VPD. A similar response was observed for leaves from *Eucalyptus tetrodonta* trees grown under ambient conditions[30]. Aphalo and Jarvis[31] also observed a linear relationship between gs and VPD in *Hedera helix* under constant Tl and $PPFD$. There were differences in responses of gas exchange to VPD between the different tree ages of aspen and between the different shoots of three ages of jack pine and black spruce. For aspen, the effect of VPD on gas exchange was only obvious in old trees. Yoder et al.[22] reported that the vascular system of *Pinus contorta* and *Pinus ponderosa* in old trees had lower hydraulic conductance than that in younger trees. The height of the old aspen trees in this study was 2～3 times that of the younger trees; a lower hydraulic conductance might relate to the their greater

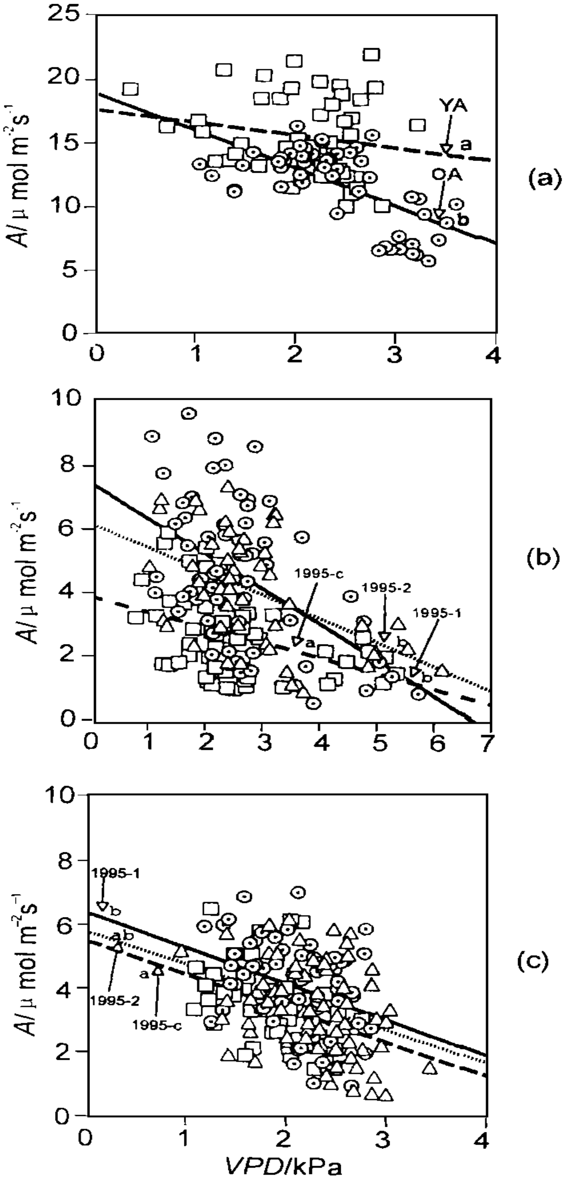

Fig. 5 The response of net CO_2 assimilation rate (A) to vapor pressure deficit (VPD) in aspen leaves and jack pine and black spruce shoots under $PPFD > 1\,000\ \mu mol\ m^{-2}\ s^{-1}$, ambient CO_2 concentration, and Ta of 25℃～29℃. Symbols represent observations of different leaves and shoots. Different letters denote significantly different values at $P < 0.05$.

(a) Young and old aspen: □ YA, ⊙ OA; (b) Jack pine: □ 1995-C, ⊙ 1995-1, △ 1995-2; (c) Black spruce: □ 1995-C, ⊙ 1995-1, △ 1995-2

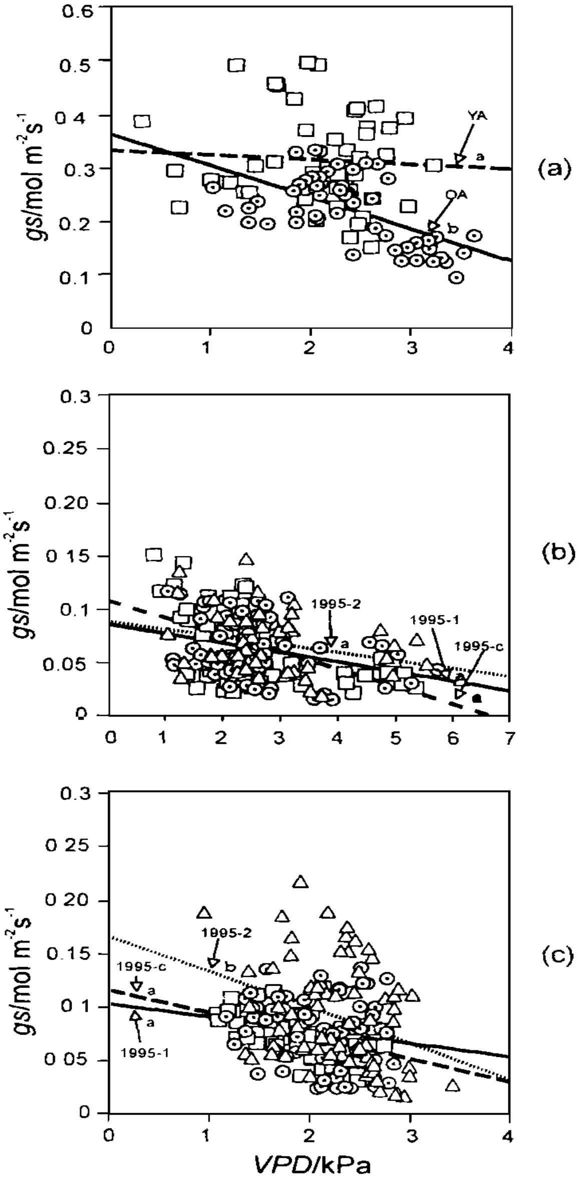

Fig. 6 The response of stomatal conductance (gs) to vapor pressure deficit (VPD) in aspen leaves and jack pine and black spruce shoots under $PPFD > 1\,000\ \mu mol\ m^{-2}\ s^{-1}$, ambient CO_2 concentration, and Ta of 25～29℃. Symbols represent observations of different leaves and shoots. Different letters denote significantly different values at $P < 0.05$.

(a) Young and old aspen: □ YA, ⊙ OA; (b) Jack pine: □ 1995-C, ⊙ 1995-1, △ 1995-2; (c) Black spruce: □ 1995-C, ⊙ 1995-1, △ 1995-2

VPD-sensitivity. However, there were insufficient data at larger *VPD* (> 3 kPa) to clearly define the shape of the response in young aspen or in black spruce. Grossnickle and Black[9] reported that *VPD* had a major influence on the stomatal opening of jack pine, black spruce and white spruce (*Picea glauca*). During boreal summers, diurnal water deficits may often occur because of high transpiration rates and simultaneously low hydraulic conductivities. Vapor pressure deficit is recognized as one of most important sources of variation in *gs*, but the mechanism of the response is presently unknown[4].

2.4 Response of gas exchange to CO_2 concentration

Responses of *A* to *Ci* for leaves of young aspen are shown in Fig. 7. Values of *Tl* and *VPD* for these determinations are shown in Table 3. The curves at different *PPFD* levels had the same form, but differed significantly in *CE*. Carboxylation efficiency increased with an increase in *PPFD*, regardless of *DOY* as did Γ. *A*-*Ci* curves under different *PPFD* levels for the different species were similar in form (Fig. 8), but also differed in *CE* and Γ (Table 4). Variations of *Tl* and *VPD* are also shown in Table 4. Carboxylation efficiency was dependent on *PPFD* for all species and increased as *PPFD* increased. However, differences in *CE* between species was large. All deciduous species had higher *CE* and lower Γ than jack pine. Among the three deciduous species (young aspen, balsam poplar and hazelnut) grown at the same site, young aspen showed the highest *CE*, balsam poplar was intermediate and hazelnut was the lowest under similar *PPFD*. There were no obvious differences in Γ among the deciduous species. Additionally, young aspen showed higher *CE* than old aspen. The effect of *PPFD* on Γ was not well defined; however, in jack pine Γ clearly decreased with increasing *PPFD*.

Conifers are characterized by lower rates of photosynthesis and lower N requirement for growth than those of deciduous species[32]. Previous studies have demonstrated that *CE* decreases at low leaf/needle N content in bean[33] and jack pine[34]. Further studies are needed to understand clearly the effects of *PPFD* on Γ between coniferous and deciduous species.

In this study, aspen (particularly young aspen) was found to have higher rate of *A* and *gs* than the other species. The high *A*, especially under full sunlight (see Fig. 1a) is related to the high *N* content (data unpublished), and hence, high levels of photosynthetic enzymes in the foliage. This is a reflection of the nutrient rich soil environment. In conjunction with high *A* is the high *gs* (Fig. 1 & 2). High *gs*, and thus, transpiration rates, can only be sustained with an adequate supply of water. The high water-holding capacities of the soils upon which aspen grows are a prerequisite for the high *gs*. High *gs* is also necessary for high

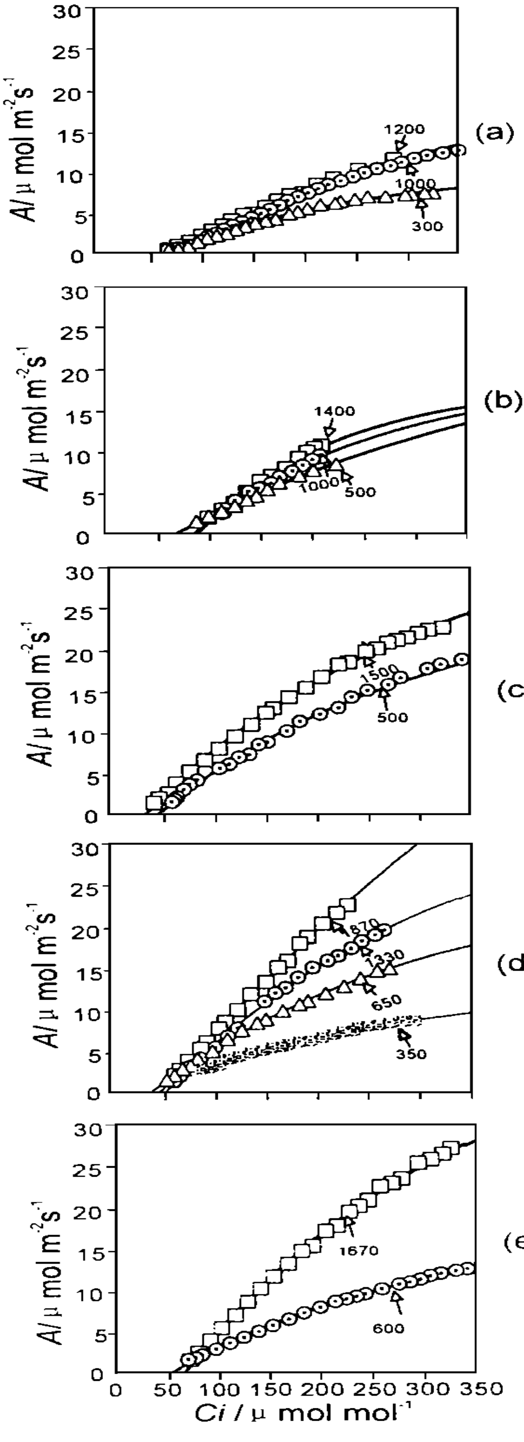

Fig. 7 Leaf CO_2 assimilation rates (*A*) of young aspen response to internal CO_2 concentration (*Ci*) at different photosynthetic photon flux density (*PPFD*) level and different day of year (*DOY*) in 1994. The arrows indicate *Ci* at ambient CO_2 concentrations (ca. 350 μ mol mol⁻¹). Each symbol represents observations on an individual leaf. Leaf temperature and *VPD* maintained in chamber are indicated in Table 3.
(a) *DOY* 167: □ 1 200, ⊙ 1 000, △ 300; (b) *DOY* 168: □ 1 400, ⊙ 1 000, △ 500; (c) *DOY* 184: □ 1 500, ⊙ 500; (d) *DOY* 205: □ 1 870, ⊙ 1 330, △ 650, ⊠ 350; (e) *DOY* 207: □ 1 670, ⊙ 600.

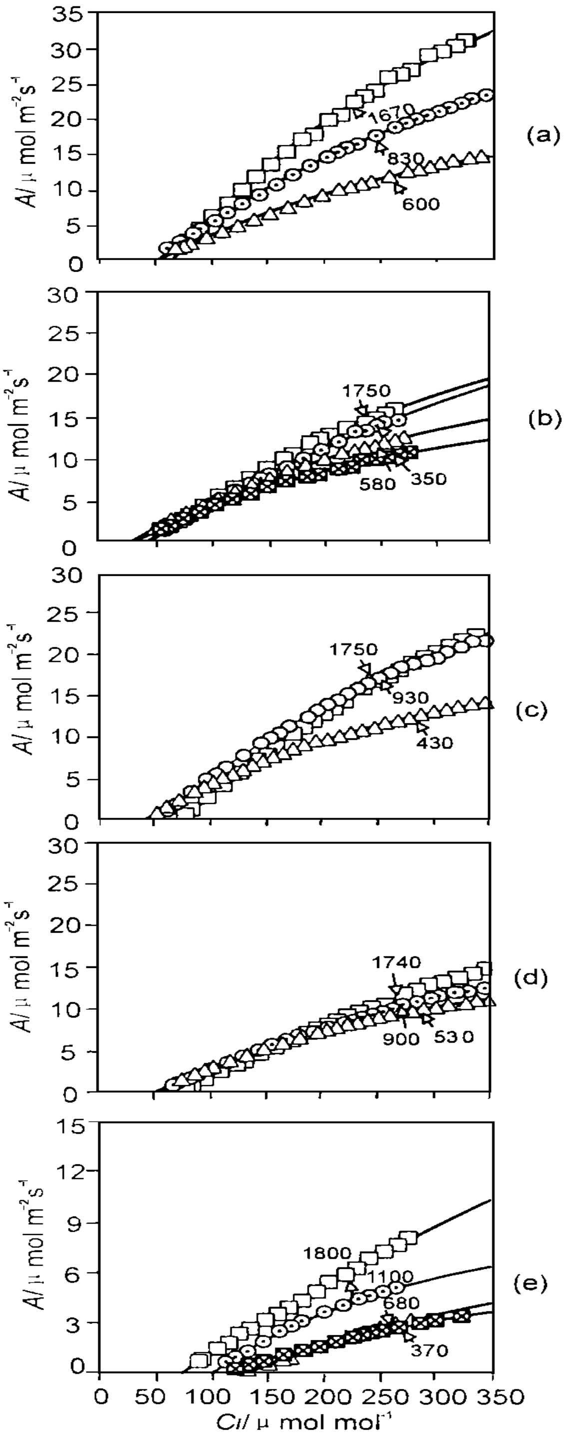

Fig. 8 Leaf/Shoot CO_2 assimilation rates (A) response to internal CO_2 concentration (Ci) at different photosynthetic photon flux density ($PPFD$) levels and different species (a) young aspen on July 26& 27 (DOY 207& 208)□ 1670, ⊙ 830, △ 600; (b) old aspen on July 25 (DOY 206)□ 1 770, ⊙ 1 660, △ 580, ⊠ 350; (c) balsam poplar on July 26& 27□ 1 750, ○ 930, △ 430; (d) hazelnut on July 26& 27□ 1 740, ⊙ 900, △ 530; and (e) jack pine on July 8& 14 (DOY 190& 195) □ 1 800, ⊙ 1 100, △ 680, ⊠ 370. The arrows indicate Ci at ambient CO_2 concentrations (ca. 350μ mol mol^{-1}). Each symbol represents observations on an individual leaf/shoot. Leaf/Shoot temperature and VPD maintained in chamber are indicated in Table 4.

Table 3 Leaf temperature (Tl) and vapor pressure deficit (VPD) during young aspen leaf A-Ci curve measurements. Data are given for selected days under different light environments. The photosynthetic parameters of CO_2 compensation point (Γ) and carboxylation efficiency (CE) were calculated using Eq (1) and the A-Ci curves in Fig. 7

DOY (M/D)	$PPFD$ (μ mol m^{-2} s^{-1})	T1 (℃)	VPD (kPa)	Γ (μ mol m^{-2} s^{-1})	CE (mol m^{-2} s^{-1})
167	1200	22.4± 0.8	1.77± 0.08	62.9	0.091
(6/16)	1000	15.5± 0.1	1.24± 0.01	68.5	0.087
	300	13.0± 0.2	0.73± 0.01	63.3	0.082
168	1400	24.9± 0.8	2.34± 0.07	87.2	0.247
(6/17)	1000	24.1± 0.9	2.17± 0.07	84.0	0.166
	500	22.6± 0.5	1.81± 0.04	65.8	0.079
184	1500	20.3± 0.1	1.26± 0.01	49.7	0.137
(7/03)	500	21.0± 0.1	1.34± 0.01	41.0	0.115
205	1870	32.4± 0.1	2.96± 0.01	52.5	0.213
(7/24)	1330	31.4± 0.1	3.16± 0.02	50.5	0.156
	650	27.2± 0.1	1.86± 0.01	35.8	0.109
	350	27.2± 0.1	2.08± 0.01	38.2	0.069
207	1670	35.6± 0.2	2.88± 0.02	63.5	0.228
(7/26)	600	28.7± 0.1	2.64± 0.02	48.6	0.099

Table 4 Leaf/shoot temperature (Tl) and vapor pressure deficit (VPD) during leaf/shoot A-Ci curve measurements. Data are given for selected days under different light environments. The photosynthetic parameters of CO_2 compensation point (Γ) and carboxylation efficiency (CE) were calculated using Eq (1) and the A-Ci curves in Fig. 8.

Species	DOY	$PPFD$ (μ mol m^{-2} s^{-1})	T1 (℃)	VPD (kPa)	Γ (μ mol m^{-2} s^{-1})	CE (mol m^{-2} s^{-1})
Old aspen	206	1770	29.1± 0.1	2.72± 0.01	50.3	0.154
		1660	27.6± 0.1	2.47± 0.01	43.1	0.124
		580	24.7± 0.1	2.07± 0.01	23.8	0.083
		350	24.4± 0.1	2.01± 0.01	27.1	0.077
Young aspen	207	1670	35.6± 0.2	2.89± 0.02	63.5	0.228
	208	830	32.0± 0.1	3.10± 0.01	48.9	0.139
	207	600	28.7± 0.1	2.64± 0.02	48.6	0.099
Balsam polpar	207	1750	34.1± 0.1	2.27± 0.02	75.8	0.166
	208	930	31.9± 0.1	2.50± 0.01	51.5	0.136
	207	430	27.4± 0.1	1.73± 0.01	37.8	0.097
Hazelnut	207	1740	35.8± 0.2	3.10± 0.02	73.4	0.092
	208	900	33.1± 0.1	2.98± 0.02	52.8	0.078
	207	530	30.7± 0.1	2.00± 0.01	46.9	0.078
Jack pine	190	1800	34.1± 0.1	3.33± 0.02	81.5	0.074
	195	1100	34.9± 0.2	2.38± 0.03	99.8	0.078
		680	35.8± 0.1	2.66± 0.08	131	0.043
		370	32.0± 0.1	2.28± 0.02	111	0.035

A. Thus the soils which support favorable growth of aspen do so by providing adequate moisture for high gs, in conjuction with high nutrient availability which leads to high A. It is interesting to note that rates of both A and gs in old aspen were smaller than those in young aspen. This may reflect decreasing availability of water and nutrients to aspen relative to other species which eventually invade the old aspen stands.

Under sandy soils conditions, Jack pine grows slow (relative to aspen) due to limitations in water and nutrient supply to roots. Results from the present study are consistent with these observations. Jack pine needle nitrogen content was low (data unpublished), as were maximum rates of net CO_2 assimilation (Table 1). Low amounts of nitrogen in the needles probably contributed to the low *A* since most of the needle N is found in the photosynthetic enzymes. Together with low *A* were the consistently low values of *gs*. Even under the most favorable conditions *gs* remained low. This may be an adaptation to the water limitations imposed by the environment. In order to conserve water, *gs* (and, hence, transpiration) is low even when moisture conditions are adequate to sustain high transpiration rates. Low *gs*, and low cuticular conductances, are also an adaptation to the severely desiccating winter environment these coniferous trees experience. In addition, available energy at the jack pine sites is partitioned more to sensible heat flux than to latent heat flux. This leads to higher canopy (and air) temperatures and higher *VPDs*. Therefore, low needle N content and low *Rd* rates (Table 1) also confer an adaptive advantage in that less fixed carbon is lost to respiratory processes.

Tolerance to flooding and low temperature are ecological characteristics that allow black spruce to dominate lowland boreal forests. Although black spruce is more tolerant of flooding than most other boreal conifers, its survival and growth are negatively affected by poor drainage in peatlands. The low N content of needles in black spruce measured in this study also reflects deficiencies in soil nutrients (data unpublished). The low N content of the foliage is also reflect in low *A* (Fig. 1) even under favorable environmental conditions. In conjunction with the low *A* are the low *gs* values for this species (Fig. 2). As with jack pine, the low *gs* may reflect an adaptation to water limitations. Although the organic soils on which black spruce grows are often water-saturated, the low oxygen availability and low temperatures most likely restrict water uptake. Also, the low hydraulic conductivities of stems and branches in this species may restrict water transport to the needles. In addition, desiccation in winter is severe. Thus low *gs*, even under favorable environmental conditions, may be a reflection of water limitations as well as a water conserving strategy. Light saturation of *A* in black spruce occurs at very low light intensities (Fig. 1). The foliage fixes carbon as well under low light as under high light. These results are also consistent with the observation that black spruce is a shade-tolerant species[6].

3 Conclusions

Our gas exchange data provide an indication of interspecific, *PPFD*, *Ta*, *VPD* and *Ci* variability in gas exchange rates and photosynthetic characteristics of these species. (1) Aspen leaves (young and old) had higher photosynthetic capacity than did shoots of jack pine and black spruce since the photosynthetic parameters, light saturation point, *Pm*, and H were higher, and *LCP* was lower as compared with those two conifers. The photosynthetic capacity was higher in young aspen than in old aspen, and in the late growing season than in the early growing season for young aspen. Stomatal conductance increased linearly with increasing *PPFD* for aspen and jack pine. For aspen under high light ($PPFD > 1\ 000\ \mu mol\ m^{-2}\ s^{-1}$), sun leaves had significantly higher gas exchange rates than did shaded leaves. (2) Air temperature had an effect on gas exchange for old and young aspen leaves and black spruce shoots but not for jack pine shoots under high light conditions. With increasing *Ta*, *A* and *gs* increased for aspen leaves and decreased for black spruce shoots. The optimum air temperatures for *A* and *gs* were 24℃~29℃ for aspen, 22℃~28℃ for jack pine and 21℃~27℃ for black spruce. However, the exact influence of *Ta* on gas exchange rates was not clearly apparent in any species. (3) The effect of *VPD* on *A* and gs was significant for old aspen leaves, jack pine and black spruce shoots. As *VPD* increased, *A* and *gs* decreased. The current-year shoots of jack pine and black spruce usually had a lower *A* than those of 1-and 2-year old shoots under the same conditions. (4) Net assimilation rates increased as *Ci* increased. As *PPFD* increased, *CE* also increased for young aspen, balsam poplar, hazelnut and jack pine. As *PPFD* increased, Γ increased in the three deciduous species while Γ decreased in jack pine. (5) The photosynthetic capacity was different among different species and different tree ages which might contribute to complex interactions between inherent physiological characteristics such as *gs* and N content, and environmental conditions such as *PPFD*, *Ta* and *VPD*. The results revealed light was the major determinant of photosynthesis under field conditions, although the rate was modified by *Ca*, *Ta* and *VPD*. Under high light, the dominant factors limiting gas exchange were *Ta* and *VPD*. The results also revealed that difference in gas exchange among different species may relate to physiological characteristics and growing conditions.

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