HORTSCIENCE 43(2):314–319. 2008.

Photosynthesis of Birch Genotypes (*Betula* L.) Under Varied Irradiance and CO_2 Concentration

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Additional index words. photosynthetic photon flux density, net assimilation rate, quantum yield, carboxylation efficiency

***Abstract*. Net CO_2 assimilation (A) of four birch genotypes (*Betula nigra* L. 'Cully', *B. papyrifera* Marsh., *B. alleghaniensis* Britton, and *B. davurica* Pall.) was studied under varied photosynthetic photon flux density (PPFD) and CO_2 concentrations (CO_2) as indicators to study their shade tolerance and potential for growth enhancement using CO_2 enrichment. Effect of water-deficit stress on assimilation under varied PPFD and (CO_2) was also investigated for *B. papyrifera*. The light saturation point at 350 ppm (CO_2) for the four genotypes varied from 743 to 1576 μmol·m^{-2}·s^{-1} photon, and the CO_2 saturation point at 1300 μmol·m^{-2}·s^{-1} photon varied from 767 to 1251 ppm. Light-saturated assimilation ranged from 10.4 μmol·m^{-2}·s^{-1} in *B. alleghaniensis* to 13.1 μmol·m^{-2}·s^{-1} in *B. davurica*. CO_2-saturated A ranged from 18.8 μmol·m^{-2}·s^{-1} in *B. nigra* 'Cully' to 33.3 μmol·m^{-2}·s^{-1} in *B. davurica*. Water-deficit stress significantly reduced the light saturation point to 366 μmol photon m^{-2}·s^{-1} but increased the CO_2 saturation point in *B. papyrifera*. Carboxylation efficiency was reduced 46% and quantum efficiency was reduced 30% by water-deficit stress in *B. papyrifera*.**

There are various light conditions in landscape situations, i.e., full sun, partial sun, or shade, and plants have different requirements for light. Photosynthetically active irradiance is an important ecological factor on which all photoautotrophic plants depend (Lambers et al., 1998). Photosynthesis is highly correlated with photosynthetic photon flux density (PPFD), and thus net carbon gain and biomass production, if other factors are optimal such as water and nutrient supply. Low PPFD could limit the photosynthesis rate in sun plants and therefore limit plant growth. High PPFD may result in photoinhibition under certain growing conditions when excess energy could not be dissipated through photochemistry (Lambers et al., 1998). Excess excitation energy may cause damage to the photosynthetic apparatus when it exceeds the capacity of other dissipation mechanism. Ambient CO_2 concentration (CO_2) is a limiting factor to net CO_2 assimilation (A) in C_3 plants (Lambers et al., 1998). Thus, increasing (CO_2) could potentially enhance photosynthesis and growth in C_3 plants. Supplemental CO_2 has been applied to improve production of vegetables or fruits in controlled environments (Edwards et al., 2004; Gao et al., 2004; Wei et al., 2004). Birch trees (*Betula* L.) are normally produced outdoors; however, vegetative propagation of some selections might benefit from supplemental CO_2 application in a greenhouse. No previous research has been conducted on CO_2 enrichment during nursery production of birch.

Light and CO_2 responses are commonly used to explore the photosynthesis mechanism of plants. Single-leaf photosynthesis measurement (Peng and Krieg, 1992) provides a good estimate of a plant's maximum photosynthetic potential, although intracanopy shading may affect the accuracy of the single leaf as an indicator of the whole-plant photosynthesis responses (Makino and Mae, 1999).

Birch consists of ≈50 deciduous species throughout the northern hemisphere (Krussmann, 1984). Birch trees are popular landscape trees for the attractive white bark, fall foliage, or pendulous catkins. Most birch trees are pioneer species in their natural habitat (Atkinson, 1992; Kobe and Coates, 1997; O'Hanlon-Manners and Kotanen, 2004) and rarely exist in the inner canopy of forests, which indicates that they may not be shade-tolerant. Previous research (Gu et al., 2003) suggested that there was a range of A under identical PPFD within the *Betula* genus. A better understanding of shade intolerance would contribute in selection and improvement among the birch trees for varied light conditions in the landscape. Although *B. papyrifera* was found to be the most shade-intolerant compared with other forest species based on models of sampling mortality in existing woods (Kobe and Coates, 1997), applying such an approach to *Betula* species in the landscape would not be feasible simply because of their diverse provenance. Four birch genotypes from diverse origins were selected for the experiment (*B. nigra* L. 'Cully' from the eastern United States, *B. papyrifera* Marsh. from North America, *B. alleghaniensis* Britton from eastern North America, and *B. davurica* Pall. from northeast China), and *B. papyrifera* was selected to study the water status effect on light and CO_2 responses resulting from its popularity in the landscape.

There have been no previous reports on light response or CO_2 response of birch genotypes. The objectives of this research were to: 1) compare light and CO_2 responses in the four birch genotypes; and 2) evaluate water status effect on light and CO_2 responses in *B. papyrifera*. The hypotheses were that there is a difference in light and CO_2 responses among the four birch genotypes and that water deficit could affect quantum efficiency and carboxylation efficiency in *B. papyrifera*, which could serve as a basis for recommending birch genotypes for landscapes with various light conditions, plant water status management in the landscape, and CO_2 enrichment for birch production under controlled environments.

Materials and Methods

Plant material and growing conditions

Four birch genotypes (*B. nigra* 'Cully', *B. papyrifera*, *B. alleghaniensis*, and *B. davurica*) obtained as rooted cuttings or bare-root plants were potted in 3.8-L pots with SunGro SB 300 Universal Mix (Pine Bluff, AR) in Winter 2003 and placed in an outdoor lathe house at the Arkansas Agriculture Research and Extension Center at Fayetteville.

The container plants were transported to the greenhouse at the Rosen Alternative Pest Control Center in June 2004. Five grams of Osmocote® 18N–2.6P–9.9K were topdress-applied to each container. Plants were grown in the greenhouse with ambient (CO_2) and

Received for publication 14 May 2007. Accepted for publication 2 Oct. 2007.
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the supplemental metal halide high-intensity discharge lights, which were automatically turned on when the ambient light level decreased to below 60 Klux. Photosynthetic photon flux density was ≈750 μmol·m^{-2}·s^{-1} photon at the upper canopy level when the supplemental lights were turned on. The greenhouse conditions were programmed at day/night temperatures of 25 ± 2/20 ± 2 °C and relative humidity of 50%. Plants were trained to a single shoot and the height of the plants was ≈1.2 m before the initiation of the experiments.

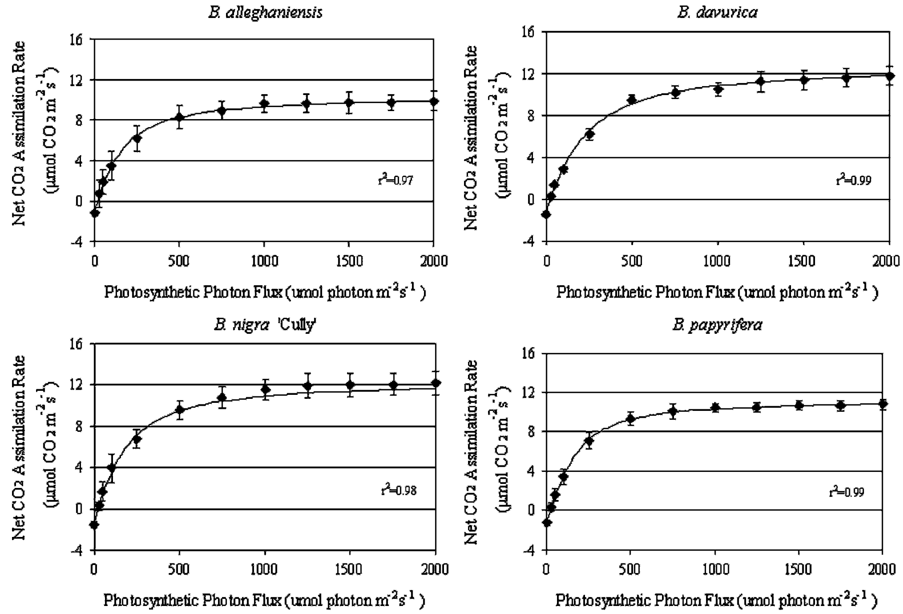

Fig. 1. Net CO_2 assimilation rate (A) in response to varied photosynthetic photon flux density (PPFD) of four birch genotypes. The cuvette conditions were set at 25 °C, 70% relative humidity, and 350 ppm (CO_2). Diamond symbols are means of six plants. Vertical bars (± SE) were shown if greater than the symbol size. Curves were predicted values from the following equations generated by SAS PROC NLIN from the measured data. *B. alleghaniensis*: $A = [0.068 \times PPFD + 11.99 - \sqrt{(0.068 \times PPFD + 11.99)^2 - 0.75 \times PPFD}]/1.00 – 1.05$; *B. davurica*: $A = [0.053 \times PPFD + 13.20 - \sqrt{(0.053 \times PPFD + 13.20)^2 - 1.40 \times PPFD}]/1.01 – 1.40$; *B. nigra* 'Cully': $A = [0.060 \times PPFD + 12.80 - \sqrt{(0.060 \times PPFD + 12.80)^2 - 1.55 \times PPFD}]/1.00 – 1.09$; *B. papyrifera*: $A = [0.052 \times PPFD + 12.14 - \sqrt{(0.052 \times PPFD + 12.14)^2 - 1.86 \times PPFD}]/1.48 – 1.10$.

Expt. 1: light response (A/PPFD) of four well-watered birch genotypes

Six trees of similar size were selected for each genotype and the experiment was conducted on the 8, 9, and 10 Sept. 2004. Gas exchange measurements were taken between 900 HR and 1330 HR (CDST; 1 to 4.5 h after sunrise) using a portable gas exchange analyzer (CIRAS-1 Analyzer; PP Systems, Haverhill, MA). The cuvette conditions were set at 25 °C and 350 ppm (CO_2). The air in the cuvette was maintained at ≈70% relative humidity to minimize stomatal heterogeneity (Griffin et al., 2004b).

Measurements were taken on a 2.5-cm^2 section on the center of the fifth unfolded leaf from the apex of each tree as described by Pettersson and McDonald (1992), and the midvein was avoided from being included in the cuvette. One measurement was taken on each leaf to get one data point in both light and CO_2 responses. Dark respiration (R_d) was recorded when the light supply unit was detached from the cuvette head and aluminum foil was used to cover the cuvette to avoid scattered radiation on the leaf (PPFD = 0 μmol·m^{-2}·s^{-1} photon). The light supply unit was replaced back to the cuvette head and irradiance increased incrementally (25, 50, 100, 250, 500, 750, 1000, 1250, 1500, 1750, 2000 μmol·m^{-2}·s^{-1} photon). After an ≈15-min acclimation period, A was recorded at each light level and fitted to the model equation

$$A = [\Phi \times PPFD + A\max - \sqrt{(\Phi \times PPFD + A\max)^2 - 4\Phi \times PPFD \times k \times A\max}]/(2k) - R_d$$

as given by Lambers et al. (1998) in which A is the net CO_2 assimilation rate, Φ is the quantum efficiency, PPFD is the incident irradiance, Amax is the light-saturated rate of gross CO_2 assimilation (light-saturated net CO_2 assimilation plus R_d) at infinitely high irradiance, and k is the curvature factor describing the convexity of the curve, which can vary between 0 and 1. When k is close to 1, the curve changes directly from the initial line determined by Φ to a plateau (called Blackman type) determined by Amax and R_d (Leverenz, 1987; Ogren, 1993). When k is close to 0, the curve is a rectangular hyperbola (Leverenz, 1987).

Light compensation point at ambient (CO_2) (350 ppm), referred to as $PPFD_{comp}$, was calculated when A was equal to 0. The value of $PPFD_{sat}$ at ambient (CO_2) was calculated as the PPFD associated with 90% of Amax like by Jurik et al. (1988). Light-saturated A at ambient (CO_2) was calculated when PPFD was equal to $PPFD_{sat}$. The PPFD associated with a 50% reduction in Amax ($PPFD_{50\%}$) was also calculated.

Expt. 2: CO_2 response [A/(CO_2)] of four well-watered birch genotypes

A/(CO_2) of each genotype was measured on the same fifth leaf between 900 HR and 1330 HR (CDST; 1 to 4.5 h after sunrise) on 11, 12, and 13 Sept. 2004. The cuvette condition started as 0 ppm (CO_2), 25 °C, 70% relative humidity, and 1300 μmol·m^{-2}·s^{-1} photon PPFD. This level of PPFD was close to the $PPFD_{sat}$ estimated from A/PPFD for the four birch genotypes. Pettersson and McDonald (1992) applied 600 μmol·m^{-2}·s^{-1} photon PPFD on *B. pendula* in a similar study, which was not adopted in this study because it was significantly lower than the sunlight level on a sunny day or the $PPFD_{sat}$ estimated in Expt. 1. (CO_2) was incrementally increased from 0 to 1100 ppm (50, 100, 200, 300, 400, 500, 600, 700, 800, 900, 1000, 1100 ppm). Net CO_2 assimilation was recorded after an ≈15-min acclimation at each (CO_2) level. Data were fitted to the negative exponential model adjusted from Reid and Fiscus (1998): $A = a(1 - e^{-bCa}) + c$, where *a* is the potential assimilation capacity, *b* is the initial slope or carboxylation efficiency, *Ca* is the ambient CO_2 concentration, and *c* is the intercept on the ordinate [A at the level when (CO_2) = 0 ppm].

CO_2 compensation point at 1300 μmol photon m^{-2}·s^{-1} PPFD, referred to as $(CO_2)_{comp}$, was calculated when A was equal to 0. The value of $(CO_2)_{sat}$ at 1300 μmol photon m^{-2}·s^{-1} PPFD was calculated in a similar way as $PPFD_{sat}$ [(CO_2) associated with 90% of *a*]. (CO_2)-saturated A at 1300 μmol·m^{-2}·s^{-1} photon PPFD was calculated when (CO_2) was equal to $(CO_2)_{sat}$. The (CO_2) associated with a 50% reduction in *a* [$(CO_2)_{50\%}$] was also calculated.

Expt 3: Effect of water status on light and CO_2 responses of *B. papyrifera*

Eight trees of *B. papyrifera* of similar size were selected for the experiment conducted on 12 and 13 Sept. 2005. Water was withheld from four randomly selected trees until the average predawn water potential ($\Psi_{predawn}$) reached ≈–2.5 MPa measured psychrometrically (Oosterhuis and Wulleschleger, 1987). A/PPFD and A/(CO_2) response curves were generated for well-watered (WW; $\Psi_{predawn}$ ≈ –0.5 MPa) and water-deficit-stressed (WS; $\Psi_{predawn}$ ≈ –2.5 MPa) *B. papyrifera* as described in Expts. 1 and 2.

Experimental designs

Expts. 1 and 2. The experimental design for A/PPFD and A/(CO_2) responses of four

Table 1. Light response and CO_2 response variables of four birch genotypes.

Parameters	Light and CO_2 response variables			
	B. alleghaniensis	*B. davurica*	*B. nigra* Cully	*B. papyrifera*
Light response variables[z]				
$PPFD_{comp}$ ($\mu mol \cdot m^{-2} \cdot s^{-1}$ photon)	17 NS[y]	22 NS	21 NS	21 NS
$PPFD_{50\%}$ ($\mu mol \cdot m^{-2} \cdot s^{-1}$ photon)	185 ab	249 a	206 ab	165 b
$PPFD_{sat}$ ($\mu mol \cdot m^{-2} \cdot s^{-1}$ photon)	1171 ab	1576 a	1297 ab	743 b
Quantum efficiency, Φ	0.049 NS	0.050 NS	0.066 NS	0.054 NS
Amax ($\mu mol \cdot m^{-2} \cdot s^{-1}$ CO_2)	11.7 b	14.2 a	14.1 a	11.9 b
Dark respiration, R_d ($\mu mol \cdot m^{-2} \cdot s^{-1}$ CO_2)	0.9 NS	1.1 NS	1.3 NS	1.1 NS
Light-saturated net CO_2 assimilation ($\mu mol \cdot m^{-2} \cdot s^{-1}$ CO_2)	10.4 c	13.1 a	12.9 ab	10.8 bc
Curvature factor, k	0.498 b	0.498 b	0.499 b	0.735 a
CO_2 response variables[x]				
$(CO_2)_{comp}$ (ppm)	61 NS	57 NS	58 NS	55 NS
$(CO_2)_{50\%}$ (ppm)	368 b	417 a	271 c	309 c
$(CO_2)_{sat}$ (ppm)	1083 b	1251 a	767 c	898 c
Carboxylation efficiency, *b*	0.0023 c	0.0020 d	0.0033 a	0.0027 b
Potential assimilation capacity, *a* ($\mu mol \cdot m^{-2} \cdot s^{-1}$ CO_2)	24.6 b	37.2 a	22.6 c	25.0 b
Intercept on the ordinate, *c* ($\mu mol \cdot m^{-2} \cdot s^{-1}$ CO_2)	–3.1 a	–3.9 c	–3.9 c	–3.5 b
CO_2 -saturated net CO_2 assimilation ($\mu mol \cdot m^{-2} \cdot s^{-1}$ CO_2)	21.5 b	33.3 a	18.8 c	21.6 b

[z]$PPFD_{comp}$, $PPFD_{50\%}$, and $PPFD_{sat}$ were calculated when assimilation was equal to 0, 50% and 90% of Amax from the model $A = [\Phi \times PPFD + A\max - \sqrt{(\Phi \times PPFD + A\max)^2 - 4\Phi \times PPFD \times k \times A\max}]/(2k) - R_d$ generated for each plant.

[y]Each number was the mean of six replicates. Means within a row followed by the same letter were not significantly different according to the protected least significant difference test at 0.05 level. Means followed by NS within a row were nonsignificant.

[x]$(CO_2)_{comp}$, $(CO_2)_{50\%}$, and $(CO_2)_{sat}$ were calculated when A was equal to 0, 50%, and 90% of *a* from the model $A = a\,(1 - e^{-bCa}) + c$ generated for each plant.

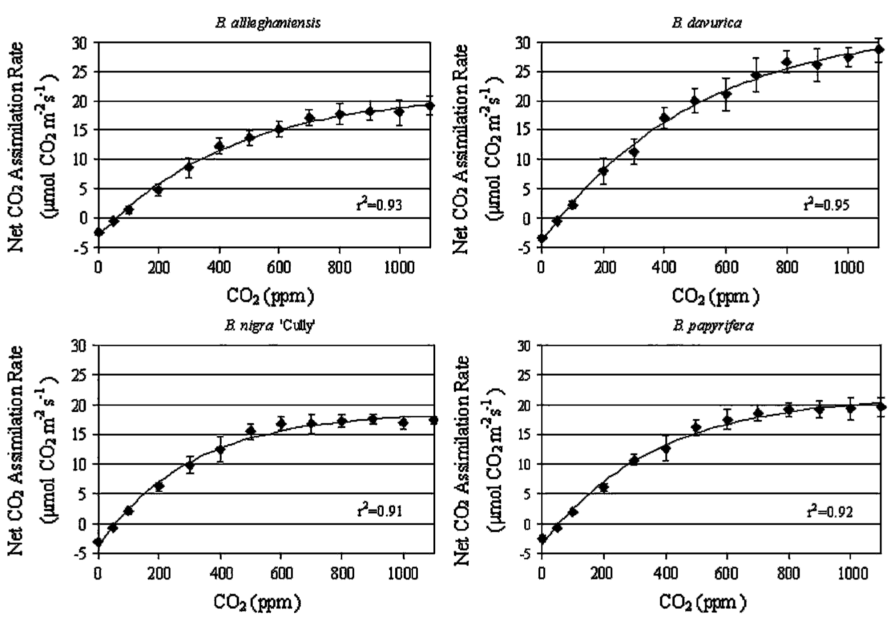

Fig. 2. Net CO_2 assimilation rate (A) in response to varied ambient CO_2 concentration (Ca) of four birch genotypes. The cuvette conditions were set at 25 °C, 70% relative humidity, and 1300 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photon photosynthetic photon flux density. Diamond symbols are means of six plants. Vertical bars (± SE) were shown if greater than the symbol size. Curves were predicted values from the following equations generated by SAS PROC NLIN from the measured data. *B. alleghaniensis*: $a = 24.46 \times (1 - e^{-0.00226Ca}) - 3.08$; *B. davurica*: $A = 36.91 \times (1 - e^{-0.00198Ca}) - 3.89$; *B. nigra* 'Cully': $A = 22.55 \times (1 - e^{-0.00329Ca}) - 3.85$; *B. papyrifera*: $A = 25.07 \times (1 - e^{-0.00273Ca}) - 3.50$.

birch genotypes was a completely randomized design with the genotype as the main factor and six replication trees per treatment. Data were subjected to SAS PROC NLIN procedure (SAS Institute, Cary, NC) to generate light and CO_2 response equations for each genotype. The variables of light and CO_2 response equation (A, Φ, Amax, R_d, *a*, *b*, and *c*) and the calculated values [$PPFD_{comp}$, $PPFD_{50\%}$, $PPFD_{sat}$, light-saturated A, $(CO_2)_{comp}$, $(CO_2)_{50\%}$, and $(CO_2)_{sat}$, (CO_2)-saturated A] were subjected to analysis of variance to investigate difference among genotypes and means were separated with a protected least significant difference at $P \leq 0.05$.

Expt. 3. Data from A/PPFD and A/(CO_2) responses of *B. papyrifera* were analyzed similarly like in Expts. 1 and 2, except with the plant water status as the main factor.

Results and Discussion

Expt. 1: A/PPFD response of four well-watered birch genotypes. There was a close relationship between PPFD and A of the four birch genotypes (r^2 = 0.97–0.99, Fig. 1). In the four birch genotypes, net CO_2 assimilation increased linearly at low PPFD, where it was limited by electron transport rate, and gradually reached a plateau where A would be limited by Rubisco capacity (Ogren, 1993). Detectable decrease in assimilation at high PPFD, an indication of photoinhibition, was not observed in any of the four genotypes for the PPFD range studied (0 to 2000 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photon). Therefore, all data were used for analysis of the relationship between PPFD and A.

The four birch genotypes reached $PPFD_{comp}$ at ≈20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photon (Table 1). The $PPFD_{comp}$ was similar for the four genotypes. Net CO_2 assimilation increased rapidly as PPFD was increased from 0 to ≈200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photon (≈10% of full sunlight), where four birch genotypes reached $PPFD_{50\%}$. $PPFD_{sat}$ occurred from 743 to 1576 $\mu mol \cdot m^{-2} \cdot s^{-1}$ photon (Fig. 1; Table 1), which is ≈30% to 70% of full sunlight. $PPFD_{50\%}$ and $PPFD_{sat}$ were significantly different among the four birch genotypes. $PPFD_{50\%}$ and $PPFD_{sat}$ of *Betula davurica* were 51% and 112% greater than *B. papyrifera*, respectively.

There were no differences in the photosynthetic quantum efficiencies (Φ) among the four genotypes (Table 1), which indicated that the four birch genotypes use light in photochemistry at similar efficiency at low irradiance when Rubisco is saturating and light is the limiting factor of photosynthesis.

The light response variables of *B. papyrifera* were similar to a previous study (Gu et al., 2003). No difference was detected for R_d among the genotypes, which ranged from 0.9 $\mu mol \cdot m^{-2} \cdot s^{-1}$ CO_2 in *B. alleghaniensis* to 1.3 $\mu mol \cdot m^{-2} \cdot s^{-1}$ CO_2 in *B. nigra* 'Cully'. The birch genotypes differed in light-saturated A and Amax (Table 1). *Betula davurica* and *B. nigra* 'Cully', which had greater $PPFD_{50\%}$ and $PPFD_{sat}$, had greater Amax and light-saturated A than *B. alleghaniensis* and

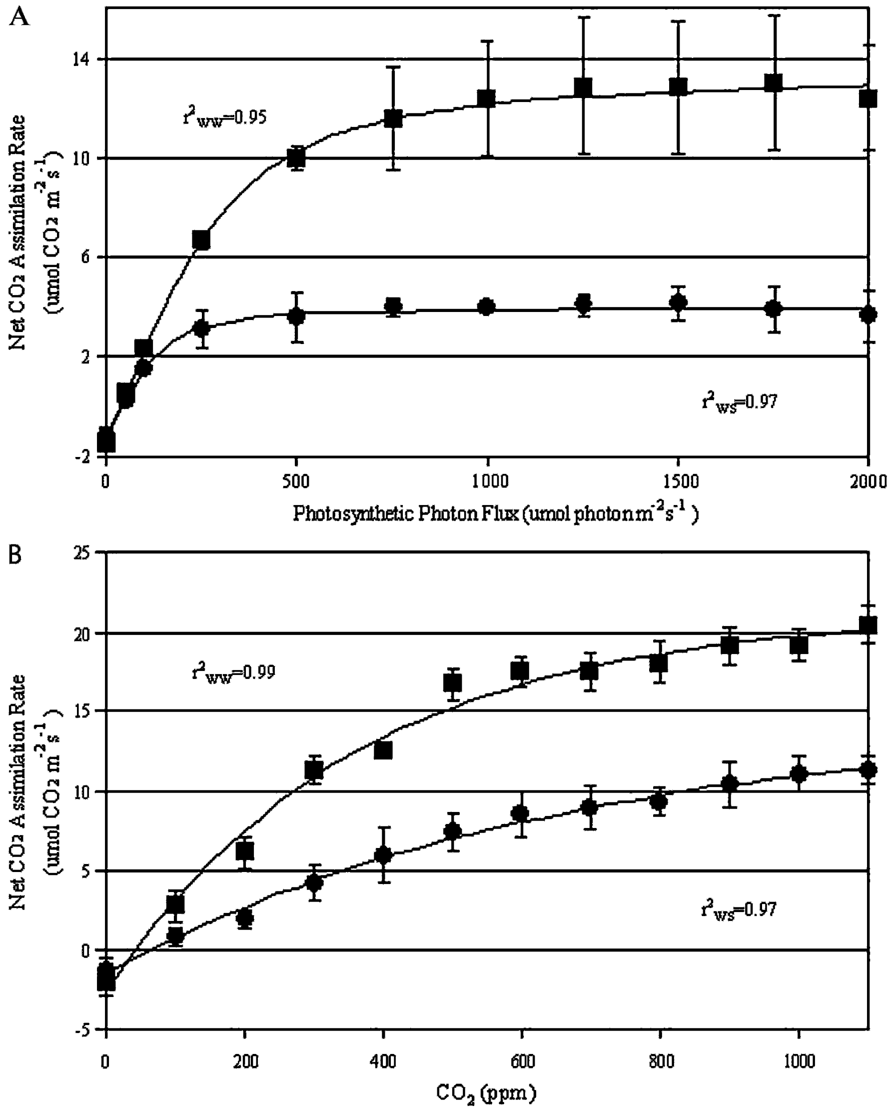

Fig. 3. Net CO_2 assimilation (A) in response to (a) varied photosynthetic photon flux density (PPFD) and (B) ambient CO_2 concentrations (Ca). The cuvette condition in (A) were set at 25 °C, 70% relative humidity, and 350 ppm (CO_2). The cuvette conditions in (Bb) were set at 25 °C, 70% relative humidity, and 1300 μmol·m^{-2}·s^{-1} photon PPFD of well-watered (WW; ■) and water-deficit-stressed (WS; ●) *B. papyrifera*. Data represented means of four plants. Vertical bars (± SE) were shown if greater than the symbol size. Curves were predicted values from the following equations generated by SAS PROC NLIN from the measured data. Well-watered *B. papyrifera*: $A = [0.039 \times PPFD + 14.91 - \sqrt{(0.039 \times PPFD + 14.91)^2 - 1.90 \times PPFD}]/1.62 - 1.42$; and $A = 23.93 \times (1 - e^{-0.00275Ca}) - 2.63$. Water-deficit-stressed *B. papyrifera*: $A = [0.031 \times PPFD + 5.26 - \sqrt{(0.031 \times PPFD + 5.26)^2 - 0.55 \times PPFD}]/1.67 - 1.21$; and $A = 15.99 \times (1 - e^{-0.00153Ca}) - 1.57$.

B. papyrifera. *Betula davurica* and *B. nigra* 'Cully' are from warmer origins than *B. alleghaniensis* and *B. papyrifera*, which could have affected their light response. Amax of *B. papyrifera* (11.9 μmol·m^{-2}·s^{-1} CO_2) was similar to a previous report (Jurik et al., 1988). Amax of *B. davurica* and *B. nigra* 'Cully' (14.2 and 14.1 μmol·m^{-2}·s^{-1} CO_2 , respectively) was ≈20% higher than those of *B. alleghaniensis* and *B. papyrifera*. Higher $PPFD_{sat}$ and Amax in *B. davurica* and *B. nigra* 'Cully' indicates their ability to convert a greater portion of the absorbed light energy to photochemistry and may lower the amount of excess energy needed to be dissipated by plants, as indicated in a similar study on *Illicium* (Griffin et al., 2004a). The greater ability observed in *B. davurica* and *B. nigra* 'Cully' to make use of sunlight than *B. alleghaniensis* and *B. papyrifera* might enable them to grow faster under full sun situations in the landscape and was consistent with field evaluation at Fayetteville, AR (Gu et al., 2007). On the other hand, the fact that *B. alleghaniensis* and *B. papyrifera* reached $PPFD_{sat}$ and Amax sooner indicated that they are more suitable for landscape situations with lower light levels than *B. davurica* and *B. nigra* 'Cully'.

Light compensation point ($PPFD_{comp}$), R_d, and Amax are significantly greater in high-light-acclimated plants compared with low-light-acclimated plants (Lambers et al., 1998). This experiment did not find significant differences in $PPFD_{comp}$ or R_d among four birch genotypes. However, $PPFD_{sat}$ of *B. davurica* and *B. nigra* 'Cully' were significantly higher than *B. alleghaniensis* or *B. papyrifera*, which might indicate their lower shade-tolerance level. Although it was found to be the most shade-intolerant compared with other forest species (Kobe and Coates, 1997), *B. papyrifera* might not be the most shade-intolerant among *Betula* species based on the A/PPFD response under greenhouse conditions.

The value of curvature factor (k) determines the photosynthetic efficiency in the intermediate light range above the linear region (Ogren, 1993). The position of the breaking points between the two limits (electron transport rate and Rubisco capacity) determines k, and the Rubisco limitation/light saturation setting at low light levels could result in a higher value of k (Ogren, 1993). *Betula papyrifera* had a significantly greater k value than the other genotypes (Table 1), which was consistent with the observation that *B. papyrifera* reached Rubisco limitation/light saturation faster (as indicated by $PPFD_{sat}$) than the other three genotypes.

Expt 2: A/(CO_2) responses of four well-watered birch genotypes. At 1300 μmol·m^{-2}·s^{-1} photon PPFD, the net CO_2 assimilation of four birch genotypes increased rapidly to a value of 15 to 20 μmol·m^{-2}·s^{-1} CO_2 with the cuvette (CO_2) elevated to 700 ppm (Fig. 2). The A/(CO_2) responses indicated that initial linear regions at low (CO_2) were Rubisco-saturated and CO_2-limited, which changed to CO_2-saturated and Rubisco-limited regions at high (CO_2) (Farquhar and Sharkey, 1982).

The $(CO_2)_{comp}$, which was not significantly different among the four genotypes, was reached at ≈60 ppm (Table 1). This was similar to a previous report on *B. pendula* under 600 μmol·m^{-2}·s^{-1} photon PPFD (Pettersson and McDonald, 1992). The $(CO_2)_{50\%}$ was significantly different among the four birch genotypes. *Betula nigra* 'Cully' and *B. papyrifera* had the lowest $(CO_2)_{50\%}$, 271 ppm and 309 ppm, respectively. *Betula davurica* had the greatest $(CO_2)_{50\%}$ of 417 ppm. At 1300 μmol·m^{-2}·s^{-1} photon PPFD, *B. davurica* had the greatest $(CO_2)_{sat}$, which was 63% higher than *B. nigra* 'Cully' (Table 1).

The carboxylation efficiency, *b*, was negatively correlated with $(CO_2)_{50\%}$ and $(CO_2)_{sat}$ in four birch genotypes (Table 1). *Betula nigra* 'Cully', which had the greatest value of *b* (0.0033) and reached the CO_2-saturated stage faster than the other three genotypes, had the lowest $(CO_2)_{50\%}$ and $(CO_2)_{sat}$. It also had the lowest *a* (potential assimilation capacity) and CO_2-saturated A (22.6 and 18.8 μmol CO_2 m^{-2}·s^{-1}, respectively). By contrast, *B. davurica*, which had the lowest value of *b* (0.0020) and reached CO_2-saturated stage slower, had the greatest $(CO_2)_{50\%}$ and $(CO_2)_{sat}$. Promotion of assimilation by increasing (CO_2) would be more detectable on *B. davurica* relative to the other genotypes. The greatest $(CO_2)_{50\%}$ (417 μmol CO_2 m^{-2}·s^{-1}) and $(CO_2)_{sat}$ (1251 μmol·m^{-2}·s^{-1} CO_2) associated with *B. davurica* allowed it to continue CO_2 assimilation at high (CO_2), whereas the other three birch genotypes could not. *Betula davurica* had the greatest *a* (37.2 μmol·m^{-2}·s^{-1} CO_2). *Betula davurica*, which had the greater Amax in the light response experiment, had the CO_2 assimilation 60% greater than the other three genotypes at $(CO_2)_{sat}$. On the contrary, *Betula nigra* 'Cully', which also had the greatest Amax in light response, had the least assimilation at $(CO_2)_{sat}$.

Birch selections such as *B. nigra* 'Cully' are usually vegetatively propagated in controlled environments before planted outside, which made CO_2 enrichment possible during the early stage of propagation. This might also be applicable to the other vegetatively propagated birch selections such as *B* × 'Royal Frost', *B. nigra* 'BNMTF', *B. pendula* 'Laciniata', and *B. platyphylla* 'Fargo' and selections of the other woody ornamental genera.

Expt. 3: Light and (CO_2) responses [A/PPFD and A/(CO_2)] of well-watered and water-deficit-stressed B. papyrifera. Well-watered plants had significantly greater A than WS plants under PPFD from 100 to 2000 μmol·m^{-2}·s^{-1} photon (Fig. 3A). Amax and light-saturated A of WW plants (15.4 and 14.0 μmol·m^{-2}·s^{-1} CO_2) were ≈3 times greater than WS plants (5.3 and 4.0 μmol CO_2 m^{-2}·s^{-1}; Table 2). Water-deficit stress did not affect $PPFD_{comp}$. $PPFD_{50\%}$ and $PPFD_{sat}$ of WW plants and values were approximately twice as high as the values for WS plants. Calculated Φ was greater in WW plants than WS plants. There was no significant effect on R_d or k between WW and WS plants. Therefore, although WW plants reached light saturation stage faster than WW plants, water-deficit stress did not significantly affect the starting point (determined by the R_d) or the shape (determined by k) of A/PPFD curve. Water-deficit-stressed plants reached light saturation at 366 μmol·m^{-2}·s^{-1} photon under 350 ppm (CO_2), which is ≈20% of full sun conditions. Full sun conditions would more likely cause photoinhibition in WS than WW plants, which reached light saturation at 752 μmol·m^{-2}·s^{-1} photon. Under full sun conditions in the landscape, WS *B. papyrifera* might experience one more stress, photoinhibition stress, than WW plants in addition to water deficit.

WW plants had significantly greater A than WS plants under (CO_2) from 100 to 1100 ppm (Fig. 3B). Potential assimilation capacity (*a*), CO_2-saturated net CO_2 assimilation, and *c* of WW plants were ≈1.5 times greater than WS plants (Table 2). $(CO_2)_{comp}$ was similar for both WW and WS plants (70 and 43 ppm, respectively). $(CO_2)_{50\%}$ of WW plants was approximately twice as high as WS plants and $(CO_2)_{sat}$ was half of WS plants. The *b* value was greater in WW plants than WS plants. Water deficit might have impaired the ability to respond actively to increased CO_2 level through both stomatal closure and other nonstomatal regulations. Sage (1994) suggested that stomata would become more conservative under water-deficit stress in elevated CO_2 environments. Therefore, water status of plants might be one key factor for successful CO_2 enrichment programs to promote plant photosynthesis and growth in controlled environments.

Table 2. Light response and CO_2 response variables of well-watered and water-deficit-stressed *B. papyrifera*.

Parameters	Light and CO_2 response variables: Well-watered	Water-deficit-stressed	Significance of F-test (0.05)[z]
Light response variables[y]			
$PPFD_{comp}$ (μmol·m^{-2}·s^{-1} photon)	40	37	NS
$PPFD_{50\%}$ (μmol·m^{-2}·s^{-1} photon)	268	133	sig.
$PPFD_{sat}$ (μmol·m^{-2}·s^{-1} photon)	752	366	sig.
Quantum efficiency, Φ	0.040	0.028	sig.
Amax (μmol·m^{-2}·s^{-1})	15.4	5.3	sig.
Dark respiration, R_d (μmol·m^{-2}·s^{-1} CO_2)	1.4	1.2	NS
Light-saturated net CO_2 assimilation (μmol·m^{-2}·s^{-1} CO_2)	14.0	4.0	sig.
Curvature factor, k	0.802	0.779	NS
CO_2 response variables[x]			
$(CO_2)_{comp}$ (ppm)	70	43	NS
$(CO_2)_{50\%}$ (ppm)	546	292	sig.
$(CO_2)_{sat}$ (ppm)	871	1651	sig.
Carboxylation efficiency, *b*	0.0028	0.0015	sig.
Potential assimilation capacity, *a* (μmol·m^{-2}·s^{-1} CO_2)	23.9	16.4	sig.
Intercept on the ordinate, *c* (μmol·m^{-2}·s^{-1} CO_2)	2.7	1.6	sig.
CO_2-saturated net CO_2 assimilation (μmol·m^{-2}·s^{-1} CO_2)	21.2	14.8	sig.

[z]The results of F-test of light and CO_2 response variables were presented as not significant indicated by NS or significant indicated by sig. at 0.05 confidence interval level.

[y]$PPFD_{comp}$, $PPFD_{50\%}$, and $PPFD_{sat}$ were calculated when assimilation was equal to 0, 50%, and 90% of Amax from the model $A = [\Phi \times PPFD + A\max - \sqrt{(\Phi \times PPFD + A\max)^2 - 4\Phi \times PPFD \times k \times A\max}]/(2k) - R_d$ generated for each plant.

[x]$(CO_2)_{comp}$, $(CO_2)_{50\%}$, and $(CO_2)_{sat}$ were calculated when assimilation was equal to 0, 50%, and 90% of *a* from the model $A = a\,(1 - e^{-bCa}) + c$ generated for each plant.

Photosynthetic activity was significantly affected by water deficit in *B. papyrifera* as indicated by less assimilation in both light and CO_2 responses (Table 2). In light response, water stress decreased Φ (quantum efficiency) by 30% and Amax by 66%, and in CO_2 response, water stress decreased *b* (carboxylation efficiency) by 48% and decreased *a* by 31%, which both indicated nonstomatal limitation of assimilation under water stress. Reduction of photosynthesis by water stress was observed in field-grown soybean; however, quantum efficiency and carboxylation efficiency were unaffected by water stress (Sullivan and Teramura, 1990). The discrepancy between the two studies might result from different levels of water stress. Stomatal closure is the dominant limitation to photosynthesis at mild to moderate water stress, and decreased Rubisco content becomes the dominant limitation on photosynthesis at severe water stress (Flexas and Medrano, 2002), which may have caused decreased quantum efficiency and carboxylation efficiency in the current study ($\Psi_{predawn} \approx -2.5$ MPa). CO_2 enrichment was found to significantly increase water use efficiency in rice exposed to water stress (Baker et al., 1997). Less reduction in photosynthesis of *B. papyrifera* under a high level of (CO_2) compared with under a high light level agreed with Baker et al.'s finding that increased (CO_2) might be able to alleviate water stress or improve water use efficiency under ambient light level.

Based on our results, k, $PPFD_{sat}$ and Amax in photosynthesis light response appeared to be good indicators of shade tolerance of birch genotypes, and k is unaffected by water-deficit stress, whereas $PPFD_{sat}$ and Amax were reduced by water-deficit stress. These values could serve as a basis for recommending birch genotypes for landscapes with various light conditions in the landscape. Almost all birch species are considered shade-intolerant, and special attention might need to be paid to their shade tolerance in landscape situations. Based on our results, *B. davurica* had the highest Amax in both light and CO_2 responses among the four birch genotypes examined under greenhouse conditions. Despite its northern origin of northeastern China, active responses of *B. davurica* to a high light level and (CO_2) in the greenhouse were confirmed by field performance at two locations in Arkansas representing U.S. Department of Agriculture cold hardiness Zone 7 and 8 (Gu et al., 2007). CO_2 enrichment could potentially increase plant growth of birch genotypes in a controlled environment, and it might be important to manage water status to maximize the benefit of CO_2 enrichment.

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