Heat Tolerance of Five Taxa of Birch (*Betula*): Physiological Responses to Supraoptimal Leaf Temperatures

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Abstract. Leaf gas-exchange and chlorophyll fluorescence measurements were used as indexes for evaluating heat tolerance among five taxa of birch: paper (*Betula papyrifera* Marsh.), European (*B. pendula* Roth.), Japanese (*B. platyphylla* var. *japonica* Hara. cv. Whitespire), Himalayan (*B. jacquemontii* Spach.), and river (*B. nigra* L. cv. Heritage). Gas-exchange measurements were conducted on individual leaves at temperatures ranging from 25 to 40C. River birch maintained the highest net photosynthetic rates (P_n) at high temperatures, while P_n of paper birch was reduced the most. Further study of river and paper birch indicated that the reduced P_n at high temperatures and the differential sensitivity between taxa resulted from several factors. Inhibition of P_n at higher temperatures was due largely to nonstomatal limitations for both taxa. Increases in respiration rates, decreases in maximal photochemical efficiency of photosystem (PS) II (F_v/F_M), and possible reductions in light energy directed to PS II (F_0 quenching) were apparent for both taxa. The capacity of river birch to maintain greater P_n at higher temperatures seemed to result from a lower Q_{10} for dark respiration and possibly greater thermotolerance of the Calvin cycle as indicated by a lack of nonphotochemical fluorescence quenching with increasing temperatures. Thermal injury, as indicated by a rapid increase in minimal, dark-acclimated (F_0) fluorescence, was not evident for either paper or river birch until temperatures reached ≈49C and was similar for both taxa.

Heat stress can be a principal limiting factor in the distribution, adaptability, and productivity of wild and cultivated plants. Inhibition of growth or plant decline under supraoptimal temperatures can result from thermal effects on many physiological and developmental processes (Fitter and Hay, 1987). Net photosynthesis (P_n), in particular, is one of the most heat-sensitive processes that governs plant growth (Björkman et al., 1980). Consequently, physiological adaptation of P_n processes to high temperatures and maintenance of P_n under supraoptimal temperatures is often a key factor in the adaptability of plants to high temperatures. The optimal temperature range for P_n is usually correlated with the temperature optimum for plant growth, and both optima are typically reflective of the plant's native (evolutional origin) climate (Berry and Björkman, 1980; Björkman et al., 1980; Fryer and Ledig, 1972; Larcher, 1991; Pisek et al., 1973). As a result, studying the sensitivity of P_n to high temperatures can serve as an integrated measure and effective tool for evaluating and comparing plant adaptability to warm environments.

There is considerable variation in the thermotolerance of P_n among plants of different genera (Björkman et al., 1980), species (Hällgren, et al., 1982; Koike and Sakagami, 1985), and in some cases ecotypes and provenances (Fryer and Ledig, 1972; Tesfai et al., 1991). For example, Koike and Sakagami (1985) found that Japanese birch, a species found on more exposed sites, was able to maintain net photosynthesis at higher temperatures (40C) than monarch birch (*B. maximowicziana* Regel.), a species typically found in valleys.

Changes in chlorophyll fluorescence can serve as an indicator of stress-induced limitations of photosynthesis and can provide insights into specific physiological components of photosynthesis that are sensitive to environmental stress (Bilger et al., 1987). Chlorophyll fluorescence characteristics have also proven useful in screening plants for heat tolerance (Bilger et al., 1984; Havaux et al., 1988; Hetherington et al., 1983; Moffatt et al., 1990). The use of pulse modulation fluorimetry, in particular, permits resolution of complicated fluorescence responses into photochemical and nonphotochemical components (Schreiber and Bilger, 1987).

Because many species of birch are important nursery or forestry crops, a greater understanding of the heat tolerance of different species and the specific characteristics and mechanisms that influence heat tolerance would aid in evaluating, selecting, and improving birches for different climates.

The objectives of this project were to 1) compare responses of P_n to supraoptimal temperatures among five taxa of birch; 2) identify taxa more tolerant of high temperatures as indicated by a greater capacity to maintain photosynthesis under high temperature stress; and 3) study mechanisms contributing to variation in response of P_n to supraoptimal temperatures.

Materials and Methods

Plant material and handling. Five taxa of birch were grown and studied: 'Heritage' river birch, paper birch, European white birch, Himalayan birch, and 'Whitespire' Japanese birch. Trees were

grown outdoors in 19-liter containers on a gravel bed located at the Mountain Horticultural Crops Research Station, Fletcher, N.C. The container media consisted of milled pine bark (<13 mm) amended with 3.0 and 0.89 kg of dolomitic limestone and micronutrient fertilizer (Micromax, Grace Sierra Horticultural Products Co., Milpitas, Calif.)/m^3, respectively. Twenty eight grams of 18N–2.6P–10K slow-release fertilizer (Osmocote; Grace Sierra, Milpitas, Calif.) was surface-applied to each container in April 1991. Plants were irrigated with ≈7.6 liters of water each day by drip irrigation. Trees were 4 years old, typically multistemmed, and 1.0 to 1.2 m high. Plants were arranged in a completely randomized design with six replicate trees per taxon.

Leaf gas exchange. Gas exchange was measured on individual, attached leaves using an open-flow gas-exchange measurement system. This system consisted of a temperature-controlled cuvette (model DDG-9920, Data Design Group, LaJolla, Calif.) regulated with a temperature controller (model CN-9000, Omega Engineering, Stamford, Conn.), a CO_2 analyzer and flowmeter (model LI-6250, LI-COR, Lincoln, Neb.) configured for open flow, and a data logger (model LI-6200, LI-COR). Leaf temperature was measured using a leaf temperature thermocouple (model 6000TC, LI-COR). A system of solenoid valves (Clippard Instrument Lab, Cincinnati) and an additional temperature–relative humidity sensor (Data Design Group) were configured such that part of the incoming air stream could be diverted and routed through the additional sensor and the CO_2 analyzer to verify the incoming CO_2 and vapor pressure before it entered the cuvette. The CO_2 concentration in the cuvette was maintained at a mean of 342 ppm (6 SD) by blending (ADC gas mixer, Hoddesdon, U.K.) incoming air from two tanks with varying CO_2 concentrations (each with 21% O_2 and the balance N_2). The vapor-pressure deficit of the incoming air was controlled for each measurement by regulating the proportion of the air stream that was bubbled through water in an Erlenmeyer flask heated to 50C. The air inside the cuvette was maintained at a mean vapor-pressure deficit of 1.34 kPa (0.22 SD) for gas-exchange measurements over all temperatures. Artificial light was provided with a quartz filament lamp providing an irradiance of 1200 $\mu mol·m^{-2}·s^{-1}$ photosynthetically active radiation (PAR) at the leaf surface.

Individual plants were carefully brought indoors immediately before being measured. One leaf, the third to fifth most recently matured (late-formed), was situated inside the cuvette and allowed to acclimate for 20 min at 25C before the first measurement. The leaf temperature was then increased 5C at ≈1C/min, the leaf was allowed to acclimate for 20 min, and the next measurement was taken. This procedure was repeated until measurements had been taken at leaf temperatures of 25, 30, 35, and 40C. All plants were well watered when measured.

Dark respiration rates were measured during daylight hours for the two species (river and paper birch) that showed the greatest differences in photosynthesis at higher temperatures. The same protocol and gas-exchange measurement system was used as described for measuring leaf gas exchange in the light, except that the leaf cuvette was enclosed in aluminum foil to exclude light.

Gas-exchange measurements were conducted from 26 July to 19 Aug. 1992. During this period, the mean daily and mean daily high temperatures outdoors were 21.9 and 26.6C, respectively. Equations for calculating P_n, stomatal conductance (g_s), and concentration of internal leaf CO_2 (C_i) followed the procedure of von Caemmerer and Farquhar (1981).

Chlorophyll fluorescence measurements. Fluorescence measurements were conducted at room temperature (20 to 22C) using a pulse modulation chlorophyll fluorometer (model PAM 101,

Walz, Effeltrich, Germany). Terms and symbols used in discussing these measurements are consistent with nomenclature presented by van Kooten and Snel (1990).

Fluorescence measurements were conducted on intact leaves of paper and river birches enclosed in a temperature-controlled cuvette (described previously) with compressed air (CO_2 = 350 ppm) supplied at a flow rate of 1 liter·min^{-1}. Minimal, dark-acclimated fluorescence (F_0) was determined while applying a pulsed light at a frequency of 1.6 kHz. Maximum, dark-acclimated fluorescence (F_M) was determined with an additional saturating flash of white light at 2500 $\mu mol·m^{-2}·s^{-1}$ PAR for 0.8 sec. Maximal variable fluorescence of dark-acclimated samples (F_V) were calculated as $F_M – F_0$. Leaf temperature was adjusted and regulated as described for the gas-exchange measurements. Leaves were acclimated in the dark for 20 min at a given temperature before each measurement.

Photochemical quenching (q_P), nonphotochemical quenching (q_N), and minimal fluorescence quenching (q_0) were measured on separate leaves at 25 and 40C. After the samples were preconditioned in the dark for 20 min, F_0 and F_M were measured as described above. Following complete relaxation of fluorescence from the initial light flash, a fluorescence kinetic was induced with actinic white light at 275 $\mu mol·m^{-2}·s^{-1}$. Supplemental saturating flashes of white light (2500 $\mu mol·m^{-2}·s^{-1}$) were applied every 20 sec. After 12 min, the actinic light and saturating flashes were turned off and the subsequent light-acclimated, minimal fluorescence ($F_0´$) was determined. Quenching coefficients were calculated according to Bilger and Schreiber (1986). Values of q_P and q_N were determined at 10 min following illumination of the leaf with actinic light.

Dark-acclimated fluorescence was also measured over a range of 25 to 60C. Temperatures were increased at ≈1C/min. Measurements were taken using a pulsed measuring light at a frequency of 1.6 kHz.

Gas-exchange and fluorescence measurements were blocked over time with complete blocks consisting of one tree of each species measured in random order. Complete blocks were measured on a given day. Analysis of variance and regression analyses were conducted using SAS's general linear model procedure (SAS Institute, Cary, N.C.). Simple linear or quadratic polynomial curves were fit to the data when significant trends were identified in the regression analyses.

Results

Leaf gas exchange. Absolute and relative (percentage of maximum) P_n decreased quadratically with increasing temperatures for all taxa (Fig. 1 A and B). A significant taxon × temperature (quadratic) interaction demonstrated that, as temperatures increased, the rate of decrease in P_n varied by taxon for absolute and relative measurements. Net photosynthesis of river birch was least affected and P_n of paper birch was most affected by increasing temperatures. At 40C, there was also considerable variation in absolute and relative P_n among taxa. River birch maintained the highest absolute and relative P_n (58% of maximum), while P_n of paper birch were the lowest (28% of maximum) when evaluated at 40C. Paper birch was also the only taxon that significantly decreased in relative P_n as temperatures increased from 25 to 30C.

Stomatal conductance was affected by a significant temperature (linear) × taxon interaction. As temperatures increased, g_s decreased linearly for all taxa, except river birch, which had an increase in g_s with increasing temperature (Fig. 2A). When compared at 40C, g_s of river birch was significantly higher than g_s of the other taxa.

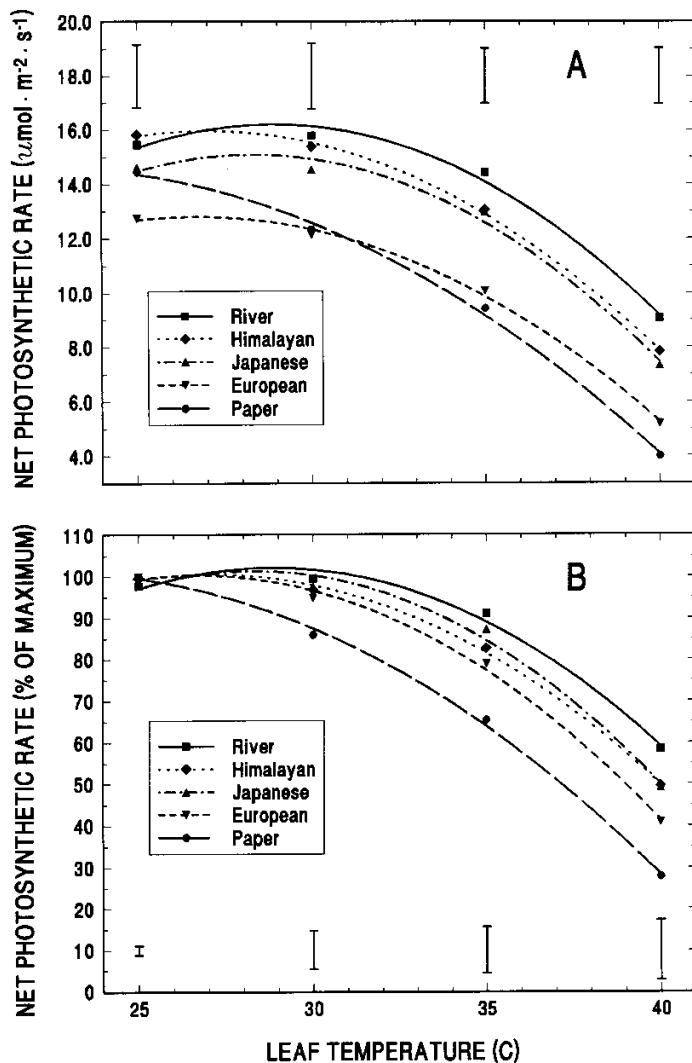Calculated C_i increased with increasing temperature for all taxa

Fig. 1. Absolute (**A**) and relative (**B**) net photosynthetic rates of five taxa of birch in response to increasing temperatures. Measurements were conducted on individual leaves after first acclimating to 25, 30, 35, or 40C for 20 min. Lines represent predicted values based on polynomial (quadratic) regression analysis. Data points represent means, with n = 6. Vertical bars represent $LSD_{0.05}$ among taxa at a given temperature.

Fig. 2. Stomatal conductance (**A**) and internal leaf CO_2 (**B**) of five taxa of birch in response to increasing temperatures. Measurements were conducted on individual, intact leaves after acclimating to 25, 30, 35, or 40C for 20 min. Lines represent predicted values based on linear regression analysis. Data points represent means, with n = 6. Vertical bars represent $LSD_{0.05}$ among taxa at a given temperature.

(Fig. 2B). There was also a significant difference in C_i among taxa. Main-effect means for C_i averaged over all temperatures were 237, 224, 223, 217, and 202 ppm for river, Japanese, European, Himalayan, and paper birch, respectively, with a least significant difference ($P \leq 0.05$) of 22. There was no significant taxon × temperature interaction effect on C_i.

Dark respiration rates increased linearly with increasing temperature, but at different rates for paper and river birches as indicated by a significant taxon × temperature interaction (Fig. 3). Although paper and river birches had similar dark respiration rates at 25C, dark respiration rates of paper birch increased at more than twice the rate of those of river birch with increasing temperatures. Temperature coefficients (Q_{10}) for dark respiration (rate at t + 10C)/(rate at tC) were 1.78 and 1.37 for paper and river birch, respectively. Because paper and river birches have similar dark respiration rates at 25C, data showed similar trends when presented on a relative basis, regardless of whether the data are expressed per unit area or per unit weight.

Chlorophyll fluorescence. As leaf temperatures increased from 25 to 40C, F_0 increased with a gradual, but significant, linear trend for both taxa (Fig. 4A). There was no significant difference in F_0
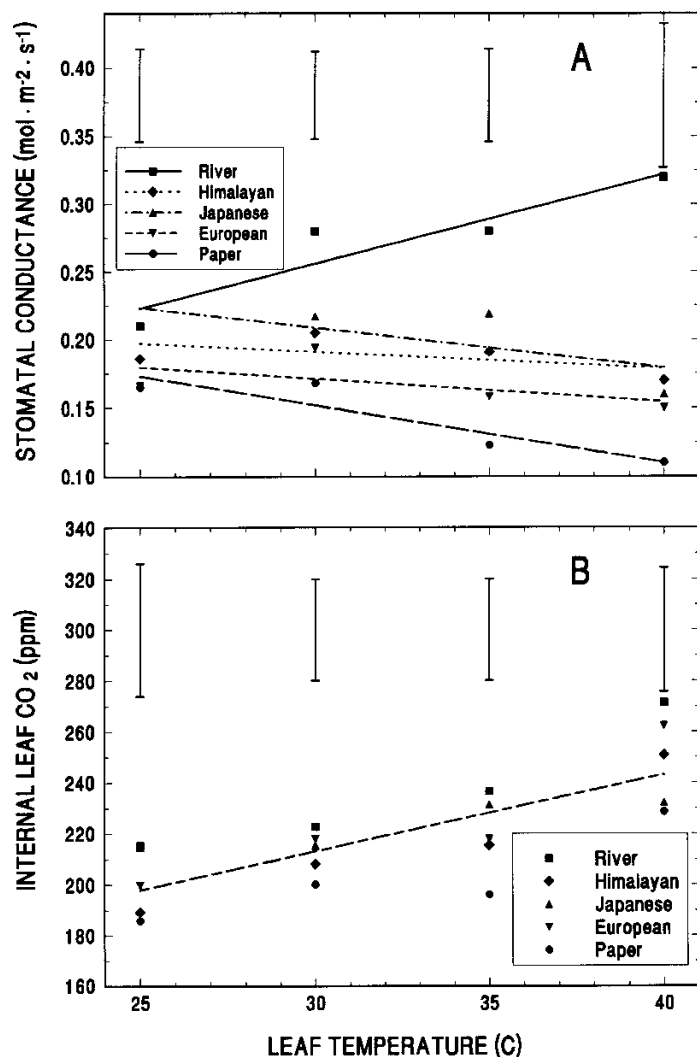
between taxa (main effect) and no taxon × temperature interaction. Maximal variable fluorescence (F_V) decreased quadratically, with no difference between taxa (main effect) and no taxon × temperature interaction. The ratio of F_V/F_M also decreased in a significant curvilinear fashion with no difference between taxa (main effect) and no taxon × temperature interaction (Fig. 4B).

Analysis of quenching coefficients showed that q_P did not differ between taxa (main effect), was not influenced by temperature (linear regression analysis), and was not influenced by taxon × temperature interactions (Fig. 5A). In contrast, there was a temperature × taxon interaction on q_N. As temperatures increased from 25 to 40C, q_N increased for paper birch and decreased for river birch. Quenching of minimal fluorescence (q_0) increased in a similar linear trend for both taxa (Fig. 5B). There was no difference in q_0 between taxa (main effect) and no significant taxon × temperature interaction.

Analysis of F_0 over a range of temperatures from 25 to 60C (Fig. 6) showed a gradual increase in F_0 between 25 and 40C followed by a sigmoidal increase in F_0 with an inflection point (T_C) near 49C. There was no significant difference in F_0 between taxa at any of the measured temperatures.

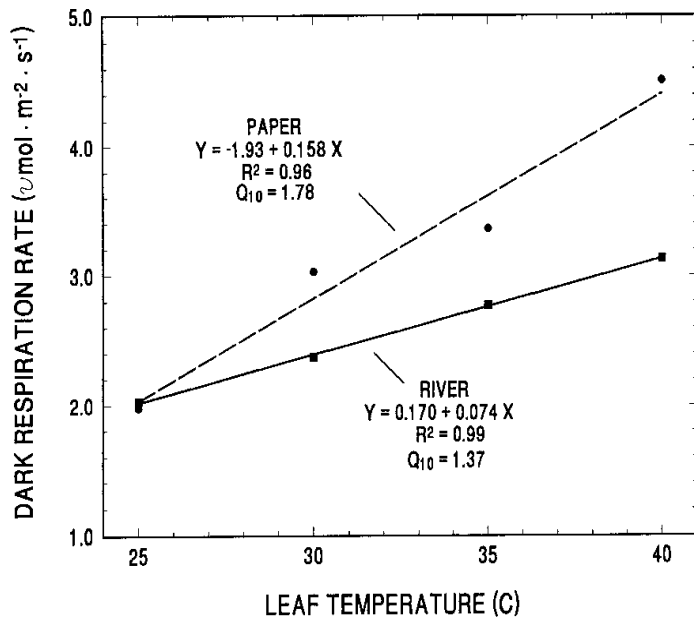J. Amer. Soc. Hort. Sci. 119(2):243–248. 1994.

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Fig. 3. Dark respiration rates as a function of increasing leaf temperature for paper and river birches. Measurements were conducted on individual, intact leaves after acclimating to 25, 30, 35, or 40C for 20 min. Data points represent means, with n = 6. Lines represent predicted values based on linear regression analysis.
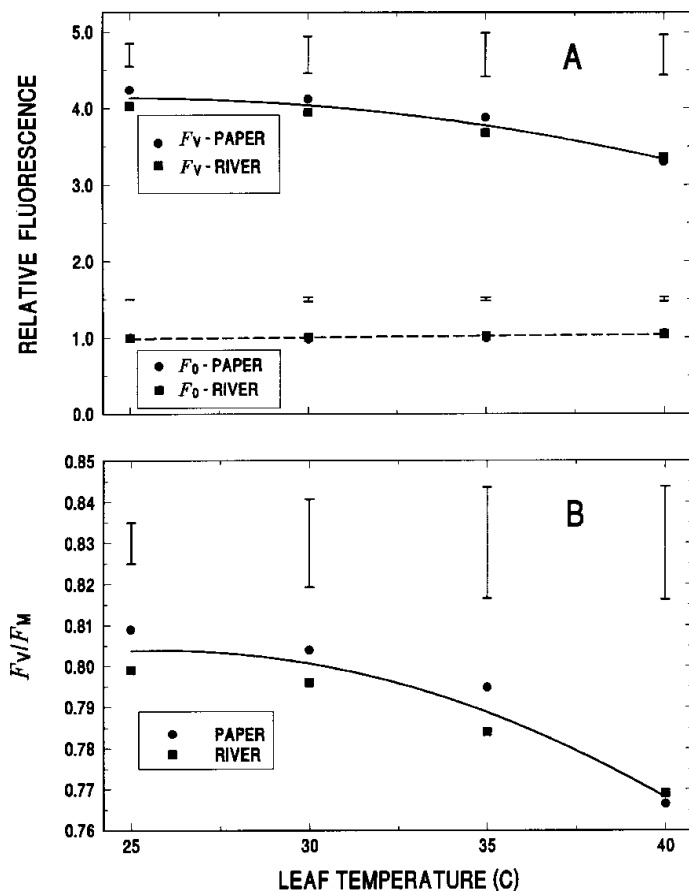

Fig. 4. Maximal variable fluorescence (F_V) and minimal, dark-acclimated fluorescence (F_0) (**A**) and maximal photochemical yield of photosystem II (F_V/F_M) (**B**), for paper and river birch in response to increasing temperatures. Measurements were conducted on individual, intact leaves after acclimating to 25, 30, 35, or 40C for 20 min. Lines in both graphs represent the predicted response based on regression analysis. Data points represent means, with n = 6. Vertical bars represent LSD$_{0.05}$ among taxa at a given temperature.
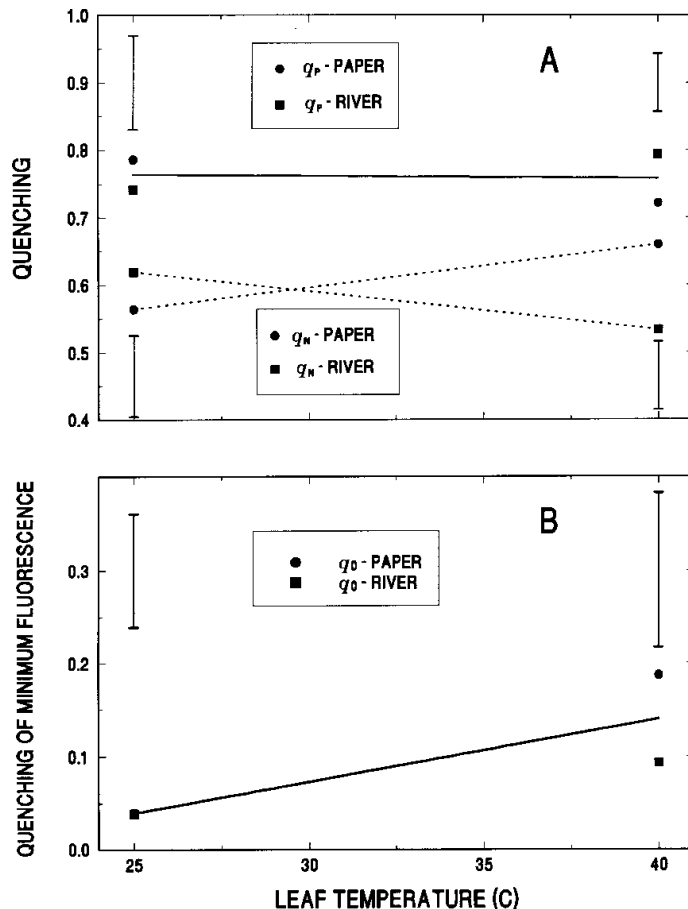

Fig. 5. Photochemical (q_P) and nonphotochemical (q_N) (**A**) and dark-level (q_0) (**B**) fluorescence quenching for paper and river birch in response to increasing temperatures. Measurements were conducted on individual, intact leaves after acclimating to 25 or 40C for 20 min. Lines connect mean values for 25C and 40C. Data points represent means, with n = 6. Vertical bars represent LSD$_{0.05}$ among taxa at a given temperature.

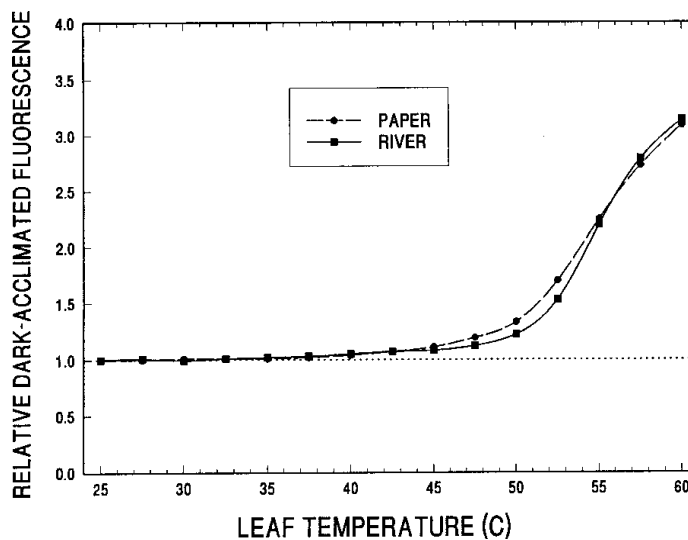Fig. 6. Relative dark-acclimated fluorescence of paper and river birch in response to increasing temperatures. Measurements were conducted on individual, intact leaves with temperatures increasing from 25 to 60C at a rate of ≈1C/min. The critical temperature (T_C) resulting in a sudden rise in F_0 was ≈49C for both species. Data points represent means, with n = 6.

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Discussion

Photosynthetic rates decreased substantially for most taxa as temperatures increased above 30C (Fig. 1 A and B). These results are similar to those reported by Koike and Sakagami (1985), who showed that photosynthetic rates of Japanese birch dropped considerably as temperatures increased in excess of 25C and ranged from ≈30% to 60% of maximum at a temperature of 40C, depending on the time of year the response was measured. Differential sensitivity of P_n to high temperatures was apparent among the five taxa (Fig. 1 A and B). Moreover, the capacity for certain taxa to maintain higher P_n (absolute and relative rates) at increasing temperatures is consistent with differences in the natural ranges of these taxa (Ashburner and Schilling, 1985; Harlow et al., 1979; Krüssman, 1984; Liberty Hyde Bailey Hortorium, 1976). River, Himalayan, and Japanese birches, which were found to maintain higher rates of P_n at supraoptimal temperatures, are native to more southern latitudes. In contrast, paper and European birches, which were found to have less ability to maintain P_n at higher temperatures, are native to more northern latitudes. The differential capacity to maintain P_n at high temperatures indicates that there is considerable variation in heat tolerance among birch species and that variations in the southernmost extent of the natural range seem to be related to tolerance of higher temperatures. Certainly, however, the possibility for intraspecific variation in heat tolerance within these species exists.

Although g_s decreased at increasing leaf temperatures for several of the taxa studied, except river birch (Fig. 2A), C_i increased for all taxa (Fig. 2B). Increased C_i most likely resulted from increased respiration rates and decreased P_n and further indicated that decreased g_s is not responsible for decreasing P_n at high temperatures. The increase in g_s at higher temperatures observed for river birch was unique among the taxa studied but has been reported for a number of other plants (Even-Chen et al., 1981; Pearcy, 1977; Schulze et al., 1974). Although g_s does not seem to be the primary factor limiting P_n at higher temperatures for any of the studied taxa, an increase in g_s would typically result in increased transpiration and enhanced evaporative cooling (Burke and Upchurch, 1989). Because river birch is a riparian plant, this species may have evolved with the capacity for increased transpiration under high temperatures, thereby minimizing leaf temperatures. However, Ranney et al. (1991) reported that g_s of river birch decreased rapidly under very mild water deficit stress, a result suggesting that increased g_s under high temperatures may only occur under high soil moisture.

Because P_n is a measurement of net CO_2 exchange, the response of P_n to increasing temperatures is strongly influenced by changes in respiration rates. River birch was found to have a Q_{10} value for leaf respiration of 1.37 (Fig. 3), similar to the Q_{10} values that Koike and Sakagami (1985) found for Japanese and monarch birches (over a range of leaf temperatures from 20 to 30C). The greater increase in respiration rates with increasing temperatures for paper birch ($Q_{10} = 1.78$) most likely contributed to a greater reduction in P_n for paper birch as temperatures increased. Dark respiration rates have often been found to be higher for plants that are not well adapted to high temperatures (Berry and Raison, 1981; Tieszen and Wieland, 1975). A rapid increase in respiration rates with increasing temperatures could in itself be a limiting factor for heat-sensitive plants due to the more rapid exhaustion of carbohydrate reserves (Crawford and Palin, 1981; Lambers, 1985), particularly under high night temperatures (Deal et al., 1990). Increased dark respiration rates can be estimated to reduce P_n by 1.1 and 2.5 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for river and paper birch, respectively, over the range

of 25 to 40C. However, in this study, P_n decreased to a greater extent for both taxa, a result indicating that increased dark respiration can only partially explain the inhibition of P_n at higher temperatures.

Chlorophyll fluorescence can serve as an intrinsic probe and sensitive indicator of stress induced limitations to photosynthesis (Bilger et al., 1987; Krause and Weis, 1984; Schreiber and Bilger, 1987). Changes in chlorophyll fluorescence for river and paper birch indicated that photochemical and possibly carboxylation efficiency were compromised at higher temperatures. Slight decreases in F_V and F_V/F_M were observed for paper and river birch at increasing temperatures (Fig. 4). The ratio F_V/F_M has been shown to be proportional to the maximum photochemical yield of PS II (Björkman, 1987; Kitajima and Butler, 1975). A reduction in photochemical yield, as found for paper and river birches at increasing temperatures, may be attributed to a number of factors including inhibition of the water-splitting apparatus (Weis, 1982; Weis and Berry, 1987). The reduction in F_V/F_M indicates reduced photochemical efficiency for both taxa, but does not seem to be responsible for the differential response of P_n at higher temperatures.

Lack of any difference in q_P when compared at 25 and 40C (Fig. 5) indicated there was little effect of these temperatures on electron transport within PS II. These results are consistent with other research results showing that electron transport of temperate plants is typically not affected by temperatures <40C (Weis, 1981). Increased q_N at increasing temperatures, as was found for paper birch, has been attributed to an increase in non-radiative de-excitation (Krause and Weis, 1984). Such an increase in q_N can reflect reduced activity of the Calvin cycle leading to reduced ATP consumption and accumulation of energy in proton gradients across the thylakoid membrane (Schreiber and Bilger, 1987). Other studies have shown that high temperatures (>20C) can interfere with the Calvin cycle due to reduced activation of RuBP-carboxylase (Weis, 1981). Quenching of dark-level fluorescence, q_0, observed for both taxa (Fig. 5B), may further suggest that there was some shift in energy distribution in favor of PS I, also resulting in reduced photosynthetic yield. Increases in q_0 have been attributed to a decrease in absorbed energy directed to PS II due to state 1 to state 2 shifts resulting from transformational changes in the light-harvesting complex (Bilger and Schreiber, 1986; Krause and Weis, 1984; Weis, 1984). Although such a transformation could limit net photosynthesis, it has been suggested that a state 1 to state 2 shift could be a protective mechanism to avoid photodamage to PS II by high light irradiance, which often accompanies heat stress (Havaux and Lannoye, 1987).

Minimal, dark-acclimated fluorescence (F_0) is typically not influenced substantially at increasing temperatures until a threshold, T_C, is reached, at which there is a sudden rise in F_0 (Fig. 6) (Schreiber and Berry, 1977). The point of inflection has been correlated with critical temperatures resulting in damage to chloroplast envelope membranes and tissue necrosis (Bilger et al., 1984; McCain et al., 1989). Although a gradual increase in F_0 was found at temperatures <40C, the increase was slight and was most likely unrelated to observed reductions in P_n. Further, T_C was ≈49C for both taxa, a result indicating the threshold for thermal injury was similar for both taxa.

Conclusion. The five taxa studied varied in their capacity to maintain photosynthesis as temperatures increased from 25 to 40C, with river birch showing the greatest tolerance and paper birch being the most sensitive. Further study of river and paper birches indicated that the inhibition of P_n at high temperatures and the differential sensitivity between taxa resulted from several

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factors. These data indicated that inhibition of P_n at higher temperatures was due largely to nonstomatal limitation for both taxa. Increases in respiration rates, decreases in maximal photochemical efficiency of PS II (F_v/F_M), and reductions in light energy directed to PS II were apparent for both taxa. The capacity of river birch to maintain greater P_n at higher temperatures seemed to result from a lower Q_{10} for dark respiration and possibly greater thermotolerance of the Calvin cycle, as indicated by lack of nonphotochemical fluorescence quenching with increasing temperatures.

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