

Foliar Heat Tolerance of Three Holly Species (*Ilex* spp.): Responses of Chlorophyll Fluorescence and Leaf Gas Exchange to Supraoptimal Leaf Temperatures

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ABSTRACT. Temperature sensitivity of CO₂ assimilation (A_{CO₂}), dark respiration, and chlorophyll fluorescence was evaluated among three taxa of hollies including *I. aquifolium* L., *I. cornuta* Lindl. & Paxt., and *I. rugosa* Friedr. Schmidt. Variations in foliar heat tolerance among these species were manifested in temperature responses for A_{CO₂}. Temperature optima of A_{CO₂} for *I. rugosa*, *I. cornuta*, and *I. aquifolium* were 22.0, 26.3, and 27.9 °C, respectively (LSD_{0.05} = 2.9). Temperature responses of respiration were similar among taxa and did not appear to be contributing factors to variations in A_{CO₂}. At 40 °C, potential photosynthetic capacity, measured under saturating CO₂, was 4.1, 9.4, and 14.8 μmol m⁻² s⁻¹ for *I. rugosa*, *I. aquifolium*, and *I. cornuta*, respectively (LSD_{0.05} = 5.1). Variations in the relative dark-acclimated fluorescence temperature curves were used to assess thresholds for irreversible heat injury. The critical fluorescence temperature threshold (T_c) was similar (48.0 °C) for all taxa. The fluorescence temperature peaks (T_p) were 52.0, 52.8, and 53.5 °C for *I. rugosa*, *I. cornuta*, and *I. aquifolium*, respectively (LSD_{0.05} = 0.9). Based on these results, *I. rugosa* was the most heat-sensitive species, followed by *I. aquifolium* and *I. cornuta*. *Ilex cornuta* also had substantially greater potential photosynthetic capacity than the other species at 40 °C, indicating superior metabolic tolerance to high temperatures.

Hollies are important landscape plants native to a broad range of latitudes, elevations, and associated climates (The New Royal Horticultural Society, 1992). Evaluation of growth and survival of hollies in warm climates suggests considerable differences in heat tolerance among species. For example, *I. cornuta* typically grows well throughout the warm climate of the southern United States, whereas *I. rugosa* grows poorly in those areas (Dirr, 1990). Many of the holly taxa that exist in commercial production are of unknown provenance and/or are hybrids between diverse taxa; thus, it is difficult to predict thermotolerance of a given cultivar based on the origin and adaptability of its respective parents.

Inhibition of growth and/or plant decline under supraoptimal temperatures can result from thermal effects on many physiological and developmental processes (Fitter and Hay, 1987). Photosynthesis is one of the most heat-sensitive processes that govern plant growth (Björkman et al., 1980). Consequently, physiological adaptation of photosynthetic processes can be a key factor in adaptability of plants to high temperatures. Temperature responses of CO₂ assimilation (A_{CO₂}) can provide an integrated measure of a plant's temperature adaptability. The optimal temperature for A_{CO₂} is usually correlated with the optimal temperature for plant growth under a given set of environmental conditions and can reflect a plant's native (evolutionary origin) climate (Berry and Björkman, 1980; Björkman et al., 1980; Friend and Helson, 1976; Fryer and

Ledig, 1972; Larcher, 1995; Pisek et al., 1973). Considerable variation occurs in the thermotolerance of A_{CO₂} among different plant genera (Björkman et al., 1980), species (Hällgren, et al., 1982; Koike and Sakagami, 1985; Moon, et al., 1987; Ranney and Peet, 1994; Ranney et al., 1995), and, in some cases, ecotypes and provenances (Fryer and Ledig, 1972; Mebrahtu, et al., 1991; Slatyer and Ferrar, 1977). When plants are acclimated to high temperatures, the optimal temperature for A_{CO₂} is a measure of the upward limit of this temperature optimum and can be used as an effective index of heat tolerance (Ranney et al., 1995).

The capacity for a plant to tolerate and survive periodic high temperature extremes can also be an important survival mechanism in certain environments. In the southern United States, foliage temperatures of hollies can exceed 50 °C (Pair and Still, 1982; J.M. Ruter, personal observation). Changes in chlorophyll fluorescence can be used as a sensitive probe for determining threshold temperatures for heat injury to the photosynthetic apparatus (Bilger et al., 1984). Minimal, dark-acclimated fluorescence (F₀) is typically stable at increasing temperatures until a critical temperature (T_c) is reached, followed by a sudden rise and peak (T_p) in F₀ (Schreiber and Berry, 1977). The values of T_c and T_p provide relative indices of progressive thermal damage to the thylakoid membrane and have been associated with an inhibition of energy transfer to the reaction centers and irreversible heat injury (Bilger et al., 1984; McCain et al., 1989; Smillie and Nott, 1979).

A greater understanding of heat tolerance of different taxa, including the specific characteristics and mechanisms that influence heat tolerance, would aid in evaluation, selection, and improvement of hollies for various climates. The objectives of this research were to 1) evaluate foliar heat tolerance of selected species of holly based on temperature responses of A_{CO₂} and critical temperature thresholds for tissue injury based on chlorophyll

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fluorescence and 2) study mechanisms contributing to variation in temperature responses of A_{CO_2} .

Materials and Methods

Three taxa of hollies, representing diverse habitats of origin, were studied, including English holly (*Ilex aquifolium* 'Monler' Sparkler), Chinese holly (*I. cornuta* 'Burfordii'), and prostrate holly (*I. rugosa*). Plants were propagated as stem cuttings from stock plants at the North Carolina State University Arboretum in Fall 1993. In April 1995, plants were transplanted into 19-L containers filled with milled pine bark amended with 2.97 kg·m⁻³ dolomitic limestone and 2.37 kg·m⁻³ fertilizer (5N-0.4P-0K, Micro-Start, Sta-Green Co., Sylacauga, Ala.). Plants were grown in an unshaded glass house with day/night temperatures of 21/18 °C, irrigated as needed, and fertilized weekly with water soluble fertilizer (20N-8.8P-16.6K; Scotts Co., Marysville, Ohio). Fertilizer solution (100 ppm N) was applied in sufficient amounts to ensure leaching. On 10 July 1995, the temperature in the greenhouse was raised to day/night temperatures of 30/25 °C to acclimate plants to warm temperatures. Plants were arranged in a completely randomized design with six replicate plants per taxon.

Gas-exchange measurements were determined on individual, attached shoots enclosed in a temperature controlled cuvette (DDG-9920, Data Design Group, La Jolla, Calif.). Leaves of all branches were from the most recent growth flush and were similar in age. Gas-exchange measurements were conducted using an open-flow gas-exchange measurement system as described by Ranney and Peet (1994). Leaf temperature was monitored using a thermocouple on the underside of a representative leaf. The CO₂ and vapor pressure deficit in the cuvette were maintained at a mean of 355 ppm (SD = 12) and 1.05 kPa (SD = 0.29), respectively, during gas-exchange measurements, regardless of temperatures. Artificial light was supplied with a quartz filament lamp providing an irradiance of 1400 μmol·m⁻²·s⁻¹ photosynthetically active radiation (400–700 nm) at the uppermost surface of a representative leaf.

Plants were maintained outside under ambient conditions before being measured. Plants were brought into a laboratory and branches with four to eight leaves were placed inside the cuvette and allowed to acclimate for 15 min at 15 °C before the first measurement. Leaf temperature was then increased 5 °C at 1 °C/min, the leaf was allowed to acclimate for 15 min, and the next measurement was taken. This procedure was repeated up to 40 °C. Equations for calculating A_{CO_2} , stomatal conductance (g_s), and calculated concentration of internal leaf CO₂ (C_i) followed von Caemmerer and Farquhar (1981). Temperature optima of A_{CO_2} for each plant were estimated by calculating the leaf temperature at which the first-order derivative of the temperature response of A_{CO_2} was equal to 0. Potential photosynthetic capacity (Larcher, 1995) at 40 °C was measured under saturating CO₂ (mean = 1216 ppm) following a 30-min acclimation period.

Dark respiration rates were measured during daylight hours. The same temperature regime protocol and gas-exchange measurement system was used as described for A_{CO_2} measurements, except that the sample cuvette

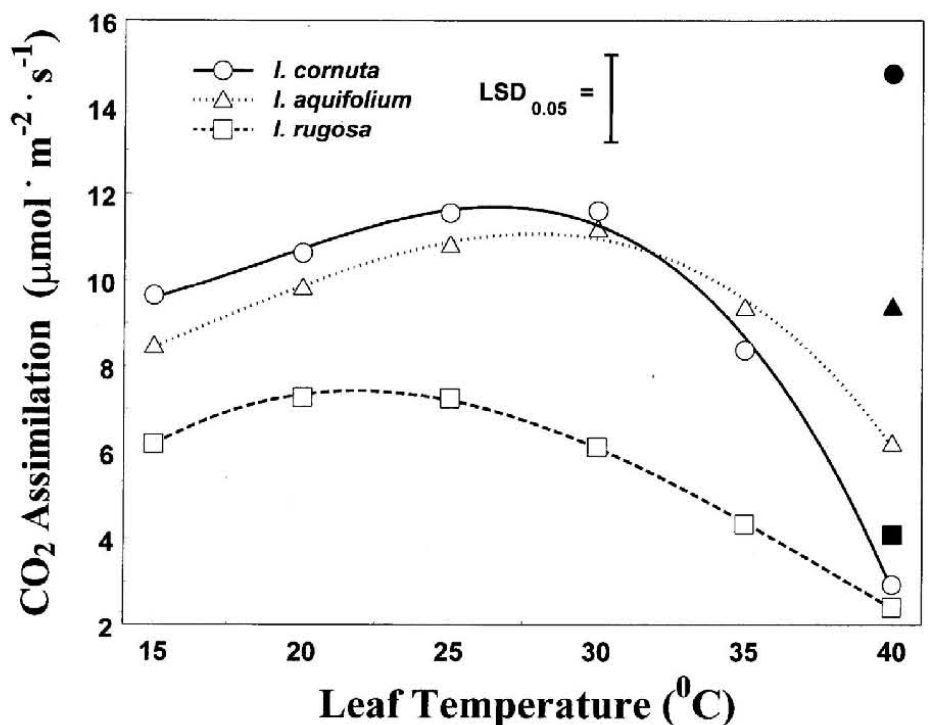
was enclosed in aluminum foil to exclude light. Dark respiration of shoots was expressed on a leaf area basis. Temperature coefficients (Q_{10}) for dark respiration were calculated as [rate at ($t + 10$ °C)]/[rate at t], where t = the base temperature used for the calculation. Separate Q_{10} coefficients were calculated for base temperatures of 15, 20, 25, and 30 °C.

Chlorophyll fluorescence was measured on individual leaves using a pulse modulation chlorophyll fluorometer (OS-500; PP Systems, Haverhill, Mass.). F_0 was measured over a range of 30 to 60 °C. Leaf temperatures were increased from 30 °C at 1 °C/min. Measurements were taken each minute using a pulsed measuring light for 10 s with 0.46 μmol·m⁻²·s⁻¹ (660 nm) at the sensor head following a 10-s far-red illumination (735 nm) of 0.0133 μmol·m⁻²·s⁻¹. T_c and T_p were calculated for each sample following Bilger et al. (1984).

Measurements were conducted from 0800 to 1700 HR from 10 Aug. through 13 Sept. 1995. For the month before and for the period during measurement, the mean daily and mean daily high temperatures in the greenhouse were 29 and 35 °C, respectively.

The experimental design was a randomized complete block with measurements of gas exchange and chlorophyll fluorescence blocked over time. Each plant was measured in random order within each of six blocks. Different branches were sampled for gas exchange in the light, dark respiration, and chlorophyll fluorescence. The treatment design was a two-way factorial with independent variables of taxa and temperature. Analysis of variance (AOV) was conducted using a general linear model (PROC GLM; SAS Institute, Cary, N.C.). Least significant difference (LSD_{0.05}) values were calculated based on a pooled mean square errors from

Fig. 1. Temperature response of CO₂ assimilation for three species of holly (*Ilex*). Open symbols are for measurements taken at 355 ppm CO₂. Solid symbols represent potential photosynthetic capacity measured under saturating CO₂ (1200 ppm). Fitted lines represent predicted responses based on regression analyses. Symbols represent means (n = 6). Vertical bars are LSD at $P < 0.05$ based on the pooled mean square error from an analysis of variance including all taxa and temperatures.



the AOV including all taxa and temperatures. Simple linear or polynomial curves were fit to the data when significant trends were identified in separate regression analyses (PROC REG; SAS) for each taxa.

Results

Temperature responses of A_{CO_2} varied by species as indicated by a significant species by temperature interaction ($P < 0.05$). Regression analysis revealed a significant cubic responses for all three taxa (Fig. 1). The temperature optima for maximum A_{CO_2} for *I. rugosa*, *I. cornuta*, and *I. aquifolium* were 22.0, 26.3, and 27.9 °C, respectively ($LSD_{0.05} = 2.9$). Mean calculated A_{CO_2} maxima (calculated from individual plant regression equations at the temperature optimum) for *I. rugosa*, *I. cornuta*, and *I. aquifolium* were 7.5, 12.1, and 11.1 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively ($LSD_{0.05} = 2.2$). Although A_{CO_2} was inhibited at 40 °C for all taxa, *I. aquifolium* maintained higher A_{CO_2} than the other two taxa. Potential photosynthetic capacity (under saturating CO_2) at 40 °C was significantly higher than A_{CO_2} at ambient CO_2 concentrations for *I. cornuta* and *I. aquifolium*, but not for *I. rugosa* (Fig. 1, solid symbols). Potential photosynthetic capacity at 40 °C was highest for *I. cornuta*, followed in descending order by *I. aquifolium*, and *I. rugosa*.

There was a significant interaction between temperature and taxa for both g_s and C_i . Temperature responses of g_s were quadratic for *I. aquifolium* and cubic for *I. cornuta* and *I. rugosa* (Fig. 2A). Temperature optima for g_s were generally similar to those for A_{CO_2} and decreased at supraoptimal temperatures. At 40 °C, *I. aquifolium* maintained higher g_s than the other two taxa. Temperature responses of C_i were cubic for *I. aquifolium* and *I. cornuta* but showed no significant trend for *I. rugosa*. At 40 °C, C_i for *I. cornuta* was significantly lower than for the other two taxa (Fig. 2B).

Dark respiration increased with increasing temperatures in a similar manner for all taxa and there were no interactions (Fig. 3). Mean values of Q_{10} for dark respiration varied from 1.9 to 2.3 over the temperature range and were similar among taxa (data not presented).

Base level fluorescence had a mean T_c of 48.0 °C and was similar for all taxa (Fig. 4). The T_p varied by taxa and was 52.0, 52.8, and 53.5 °C for *I. rugosa*, *I. cornuta*, and *I. aquifolium*, respectively ($LSD_{0.05} = 0.9$).

Discussion

Variations in A_{CO_2} among taxa indicated distinct differences in physiological tolerance to high temperatures. The greater temperature optima of A_{CO_2} for *I. aquifolium* and *I. cornuta*, above that of *I. rugosa*, indicated that the former two species had greater foliar heat tolerance, even when grown and acclimated to similar temperatures. Although the exact origin of these taxa is not known, variations in heat tolerance were consistent with the native climates of these three species. *Ilex rugosa* is a boreal (subalpine) species native to cool mountains of northern Japan (Ohwi, 1984; The New Royal Horticultural Society, 1992). *Ilex aquifolium* has a broad range extending from temperate southern and western Europe to subtropical/Mediterranean northern Africa and western Asia (The New Royal Horticultural Society, 1992). *Ilex cornuta* is native to temperate Korea and the subtropical lower Yangtze provinces in China (Hu, 1949; Hume, 1953).

Ilex rugosa was characterized by having a low temperature optimum for A_{CO_2} , a low A_{CO_2} maximum, and low g_s relative to the other taxa. At temperatures below 35 °C, low A_{CO_2} rates were most

likely related to low g_s . At these lower temperatures, g_s and C_i of *I. rugosa* were generally below 0.06 $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 160 ppm CO_2 , respectively—levels that are photosynthetically limiting for most C_3 plants (Sharkey, 1985). As temperatures were increased to 40 °C; however, A_{CO_2} decreased and C_i increased for *I. rugosa* indicating that high temperatures were directly limiting A_{CO_2} independent of g_s (Farquhar and Sharkey, 1982). Increasing CO_2 to saturating levels at 40 °C had no significant effect on A_{CO_2} of *I. rugosa*, further indicating that g_s was not limiting A_{CO_2} at high temperatures. *Ilex rugosa* is typically found as an understory plant in boreal, coniferous forests (Ohwi, 1984). In this environment, the combination of low light and desiccation stress (particularly in winter) may have resulted in the natural selection of plants having conservative water use (regulated via limited g_s) and a low A_{CO_2} capacity. Low maximal A_{CO_2} and g_s are typical of evergreen plants native to cool, alpine areas (Ranney et al., 1995; Tieszen and Wieland, 1975). Such an adaptation, however, could indirectly reduce tolerance to higher temperatures by reducing the photosynthetic efficiency coefficient (i.e., gross photosynthesis/respiration) and result in depletion of carbohydrate at higher temperatures (Crawford and Palin, 1981; Deal et al., 1990; Lambers, 1985; Larcher, 1995; Mooney, et al., 1964).

Ilex aquifolium maintained the highest A_{CO_2} at 40 °C (under ambient CO_2) and one of the highest temperature optima for A_{CO_2} . This greater A_{CO_2} , particularly at 40 °C, appeared to result from

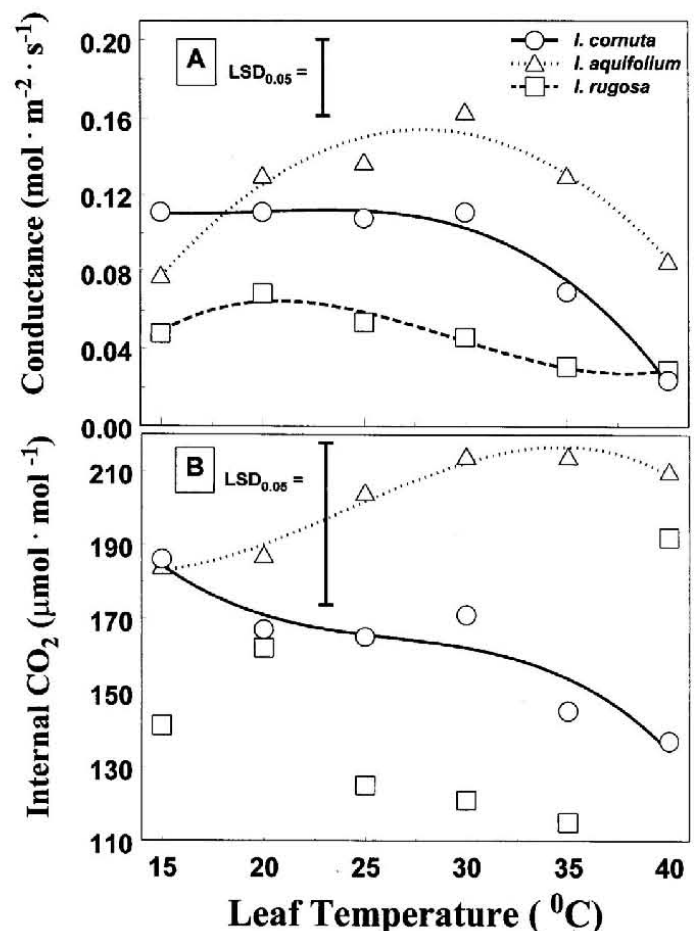


Fig. 2. Temperature response of stomatal conductance (A) and calculated internal leaf CO_2 (B) of three species of holly (*Ilex*). Fitted lines represent predicted responses based on regression analyses, when significant. Symbols represent means ($n = 6$). Vertical bars are LSD at $P < 0.05$ based on the pooled mean square error from an analysis of variance including all taxa and temperatures.

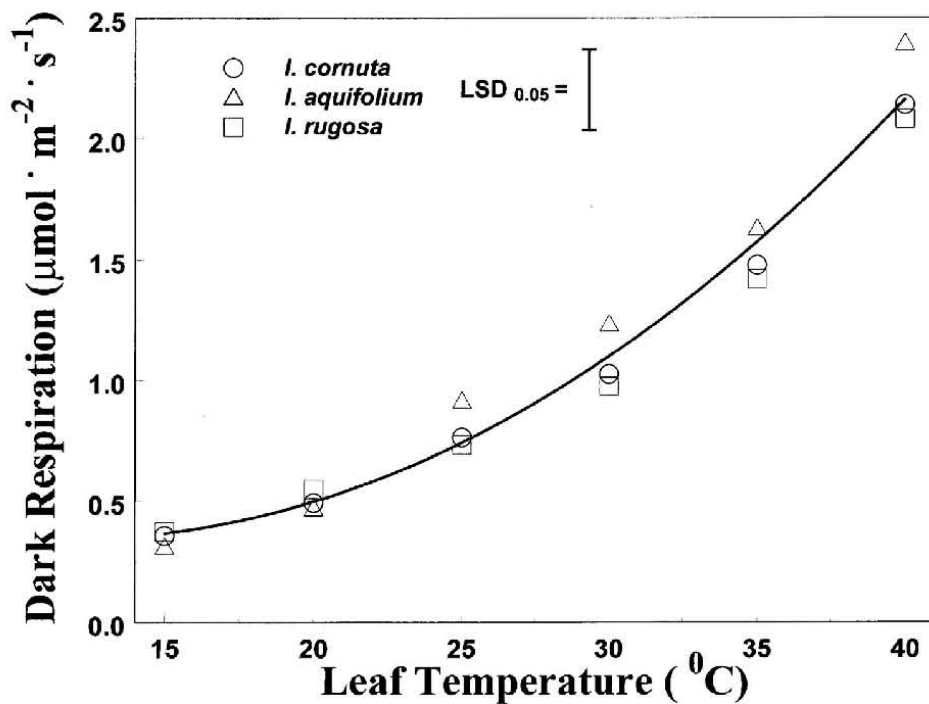


Fig. 3. Temperature response of dark respiration for three species of holly (*Ilex*). The solid line represents predicted temperature response based on regression analysis. Symbols represent means ($n = 6$). Vertical bars are LSD at $P < 0.05$ based on the pooled mean square error from an analysis of variance including all taxa and temperatures.

Ilex cornuta and *I. aquifolium* maintained significantly higher A_{CO_2} maxima than *I. rugosa*. Increased photosynthetic capacity within the optimal temperature range may also enhance heat tolerance by improving carbon balance and compensating for the higher respiratory demand experienced during warmer diurnal and seasonal periods. Photosynthetic capacity at the temperature optimum is typically greater for plants from warmer climates (Mooney and Gulmon, 1979).

Temperature responses of dark respiration were similar and did not appear to be a contributing factor to variations in A_{CO_2} . Although photorespiration was not measured in this study, the temperature dependence of photorespiration is complex and has generally not been found to be an important factor in differential temperature sensitivity of photosynthesis among taxa (Mebrahtu et al., 1991; Samuelson and Teskey, 1991).

Variations in foliar heat tolerance were not apparent based on differences in the critical temperature thresholds for tissue injury as indicated by changes in base chlorophyll fluorescence-temperature curves (T_C). However, T_p , a more extreme indicator of thylakoid perturbation, varied significantly among species. These T_p were similar to the temperature range (52–54 °C) that Ruter (1993) assessed as the critical midpoint heat killing temperature for *I. xmeserveae* S.Y. Hu 'Blue Prince' and *I. rugosa* x *I. cornuta* Lindl. & Paxt. 'Mesdob' (China Boy), based on electrolyte leakage techniques.

Results from this study indicate that *I. rugosa* was the most heat-sensitive species as indicated by a low-temperature optimum for A_{CO_2} and a low A_{CO_2} maximum. *Ilex aquifolium* and *I. cornuta* had greater heat tolerance as indicated by their higher temperature optima for A_{CO_2} and higher A_{CO_2} maxima. However, *I. cornuta* had the greatest potential photosynthetic capacity at 40 °C and saturating CO_2 , indicating superior metabolic tolerance to high temperatures.

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greater g_s , which in turn provided for greater C_i and A_{CO_2} . However, when saturating CO_2 was provided at 40 °C, the potential photosynthetic capacity of *I. aquifolium* was only intermediate between *I. rugosa* and *I. cornuta*.

Ilex cornuta had one of the highest temperature optima for A_{CO_2} , but g_s , C_i , and A_{CO_2} decreased rapidly at temperatures above 30 °C. When CO_2 was increased to saturating concentrations at 40 °C, A_{CO_2} for *I. cornuta* increased from 3 to 17 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The response indicated that these plants maintained a considerable capacity for A_{CO_2} but that stomata were primarily responsible for limiting A_{CO_2} at high temperatures and ambient CO_2 levels, despite a low vapor-pressure deficit. This decrease in g_s at high temperatures may be an adaptation for desiccation avoidance. In the Zhejiang province of China, *Ilex cornuta* grows on warm, exposed rocky hillsides where water deficit stress can be limiting (Lancaster, 1989).

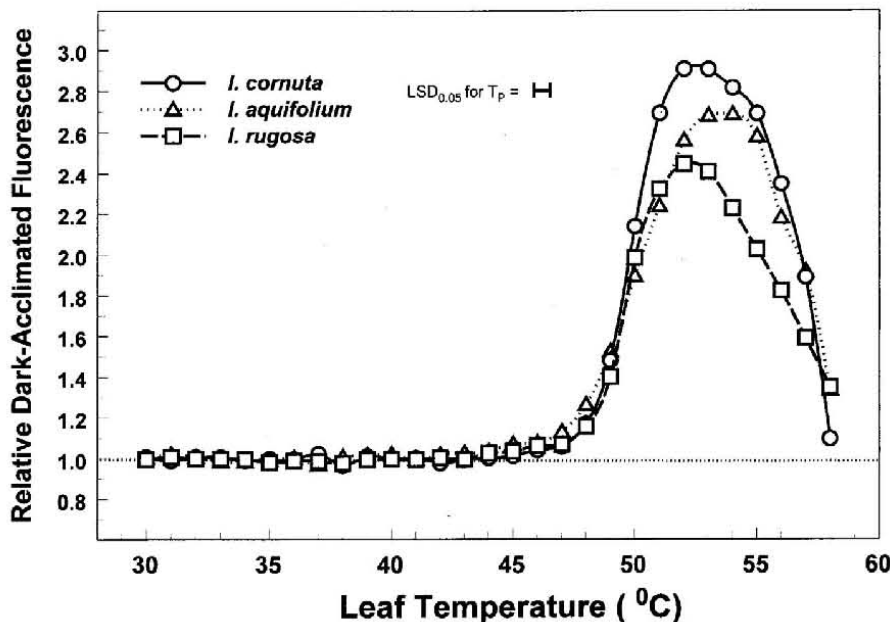


Fig. 4. Temperature response of relative dark-acclimated fluorescence (F_0) of three species of holly (*Ilex*). The critical fluorescence-temperature threshold (T_C) was similar for all taxa at 48.0 °C. The fluorescence temperature peak (T_p) varied by taxa and was 52.0, 52.8, and 53.5 for *I. rugosa*, *I. cornuta*, and *I. aquifolium*, respectively (LSD_{0.05} = 0.9). Symbols represent means ($n = 5$). Vertical bars are LSD at $P < 0.05$ based on the pooled mean square error from an analysis of variance including all taxa and temperatures.

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