Heat Tolerance of Selected Species and Populations of Rhododendron

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Abstract. **Temperature sensitivity of net photosynthesis (P_N) was evaluated among four taxa of rhododendron including *Rhododendron hyperythrum* Hayata, *R. russatum* Balf. & Forr., and plants from two populations (northern and southern provenances) of *R. catawbiense* Michx. Measurements were conducted on leaves at temperatures rauging from 15 to 40C. Temperature optima for P_N ranged from a low of 20C for *R. russatum* to a high of 25C for *R. hyperythrum*. At 40C, P_N rates for *R. hyperythrum, R. catawbiense* (northern provenance), *R. catawbiense* (southern provenance), and *R. russatum* were 7.8, 5.7, 3.5, and 0.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively ($LSD_{0.05} = 1.7$). Rhododendron catawbiense from the southern provenance did not appear to have greater heat tolerance than plants from the northern provenance. Differences in dark respiration among taxa were related primarily to differences in tissue weight per unit leaf surface area. Temperature coefficients (Q_s) for respiration did not vary in temperature response among taxa. Differences in heat tolerance appeared to result from a combination of stomatal and nonstomatal limitations on P_N at high temperatures.**

Heat stress can be a primary limiting factor in the distribution and adaptability of wild and cultivated plants. 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). Net photosynthesis (P_N), in particular, is one of the most heat-sensitive processes governing plant growth (Bjorkman et al., 1980). Consequently, physiological adaptation of photosynthetic processes to high temperatures and maintenance of high P_N under supraoptimal temperatures are often key factors in adaptability of plants to high temperatures. The optimal temperature for P_N is usually correlated with the optimal temperature for plant growth, and both optima are typically reflective of the plant's native (evolutionary origin) climate (Berry and Bjorkman, 1980; Bjorkman et al., 1980; Friend and Helson, 1976; Fryer and Ledig, 1972; Larcher, 1991; Pisek et al., 1973).

Considerable variation occurs in the thermotolerance of P_N among different plant genera (Bjorkman et al., 1980), species (Hallgren et al., 1982; Koike and Sakagami, 1985; Moon et al., 1987; Ranney and Peet, 1994), and in some cases ecotypes and provenances (Fryer and Ledig, 1972; Slatyer and Ferrar, 1977; Tesfai et al., 1991). Thus, temperature sensitivity of P_N can serve as an integrated measure and effective tool for evaluating and comparing plant adaptability to warm environments.

Evaluation of growth and survival of rhododendron *(Rhododendron* spp. L.) in warm climates suggests considerable differences in heat tolerance among species. For example, *R. hyperythrum,* an elepidote species in the Ponticum series, is native to Taiwan at elevations of 900–1200 m (Davidian, 1982b) and has grown well

in the warm climate of Louisiana (Thornton, 1989, 1990) and in greenhouse evaluations of heat tolerance among rhododendron species (Arisumi et al., 1986). In contrast, *R. russutum, is* an alpine, lepidote rhododendron in the Laponicum series, native to the northwest Yunnan province of China at elevations of 3400-4300 m and grows poorly in warmer climates (Davidian, 1982a; Leach, 1961).

The potential for selecting more heat-tolerant varieties of a given species also exists. Rhododendron catawbiense has a natural range extending through Virginia, West Virginia, North Carolina, South Carolina, Alabama, and Georgia (Leach, 196 1). Within this range, *R. catawbiense* occurs at elevations ranging from 70 to 1800 m. *Rhododendron catawbiense* from low elevations and more southern latitudes may possess greater heat tolerance that could be utilized in breeding and selecting superior plants for warmer climates.

As many species of rhododendron are important landscape plants, a greater understanding of heat tolerance of different species and provenances, as well as the specific characteristics and mechanisms that influence heat tolerance, would aid in evaluation, selection, and improvement of rhododendron for different climates. The objectives of this research were to 1) evaluate heat tolerance of selected species and populations of rhododendron based on temperature optimum of P_N and thermostability of P_N at supraoptimal temperatures and 2) study mechanisms contributing to variation in temperature response of P_N.

Materials and Methods

Plant material and handling. Four taxa of rhododendron were grown and studied, including *R. hyperythrum, R. russatum,* and plants from two populations (northern and southern provenances) of *R. catawbiense.* Seeds of *R. hyperythrum* were acquired from The American Rhododendron Society, Seed Exchange, Eugene, Ore., Lot 89-451. Seeds from a northern provenance (NP) of *R. catawbiense* were collected on Black Mountain, Pocahontas County, W.V. (38°30'N, 80°15' W, elevation = 1280 m). Seeds from a

southern, disjunct population (SP) of *R. catawbiense* were collected in Cherokee County, Ga. (34°20'N, 84°23'W, elevation = 320 m). All seeds were germinated during Winter 1990. *Rhododendron russatum* were acquired from Van Veen Nursery, Portland, Ore., in Spring 1992.

Starting in 1993, plants were grown in 19-liter containers with a medium of milled pine bark amended with 2.5 and 0.89 kg·m^{-3} dolomitic limestone and micronutrient fertilizer (Micromax, Grace Sierra Hort. Products Co., Milpitas, Calif.), respectively. Twenty grams of 18N–2.6P–10K slow-release fertilizer (Osmocote, Grace Sierra) was surface applied to each container in April 1993. Plants were grown outdoors, in full sun, on a gravel bed located at the Mountain Horticultural Crops Research Station, Fletcher, N.C. Plants were arranged in a completely randomized design with six replicate plants per taxon.

Leaf gas exchange. Gas exchange measurements were determined on individual, attached leaves for all taxa except *R. russatum.* Due to the small leaves of R. russatum, measurements were conducted on branches having 10–15 leaves. Leaves of all plants were from the most recent growth flush and were similar in age.

Gas exchange measurements were conducted utilizing an open-flow gas exchange measurement system as described by Ranney and Peet (1994). The CO_2 in the cuvette was maintained at a mean of 330 ppm (SD = 4). Vapor pressure deficit in the cuvette was maintained at a mean of 0.96 kPa (SD = 0.20) for gas exchange measurements over all temperatures. Artificial light was supplied with a quartz filament lamp providing an irradiance of 1200

$\mu mol·m^{-2}·s^{-1}$ photosynthetically active radiation (400-700 nm) at the leaf surface.

Individual plants were brought indoors immediately before being measured. Leaves were placed inside the cuvette and allowed to acclimate for 15 min at 15C before the first measurement. Leaf temperature was then increased 5C at= 1 C rein, the leaf was allowed to acclimate for 15 rein, and the next measurement was taken. This procedure was repeated until measurements had been taken at leaf temperatures of 15, 20, 25, 30, 35, and 40C. All plants were irrigated before measurements.

Dark respiration rates were measured during daylight hours. The same protocol and gas exchange measurement system was used as described for measurement of leaf gas exchange in the light with the exception that the sample cuvette was enclosed in aluminum foil to exclude light. Temperature coefficients (Q_5) for dark respiration were calculated as [rate at (t + 5C)/(rate at t)], where t = the base temperature used for the calculation.

Gas exchange measurements were conducted from 30 Aug. to 23 Sept. 1993. Each plant was measured in random order, once in the light and once in the dark. For the 2 months before measurement, the mean daily, mean daily high, and highest temperatures outdoors where plants were-growing were 23.4, 29.6, and 36.7C, respectively. Equations for calculating P_N, stomata] conductance (g_s), and calculated concentration of internal leaf CO_2, (C_i) followed von Caemmerer and Farquhar (1981). Gross photosynthesis was estimated as the sum of P_N and dark respiration and did not include estimates of photorespiration.
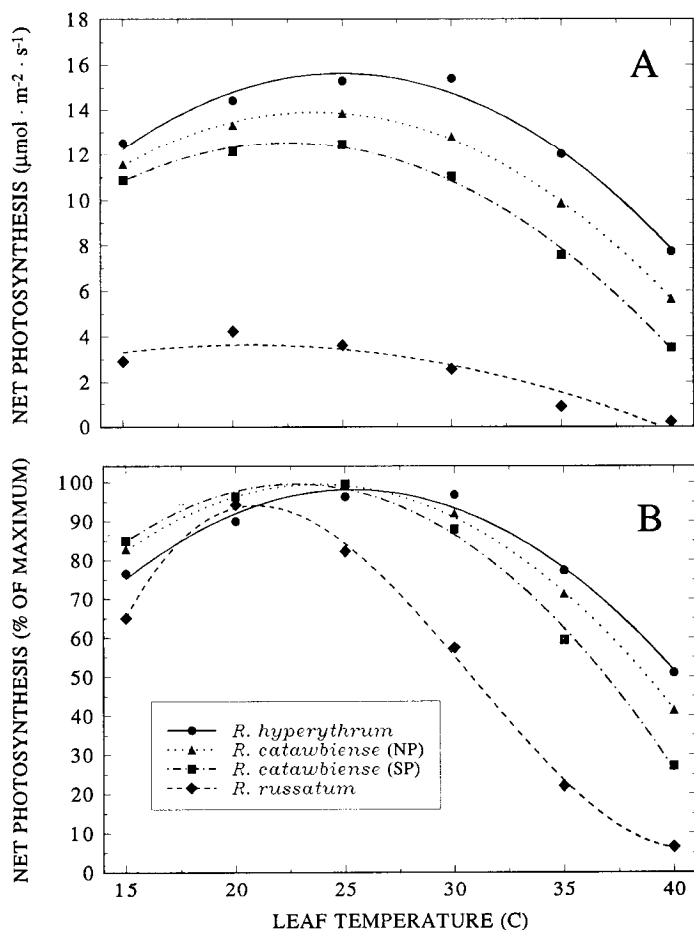

Fig. 1. Absolute (A) and relative (B) net photosynthetic rates of four taxa of rhododendron in response to increasing temperatures. Lines represent predicted responses based on regression analyses. Symbols represent means, with n = 6. NP = northern provenance, SP = southern provenance.
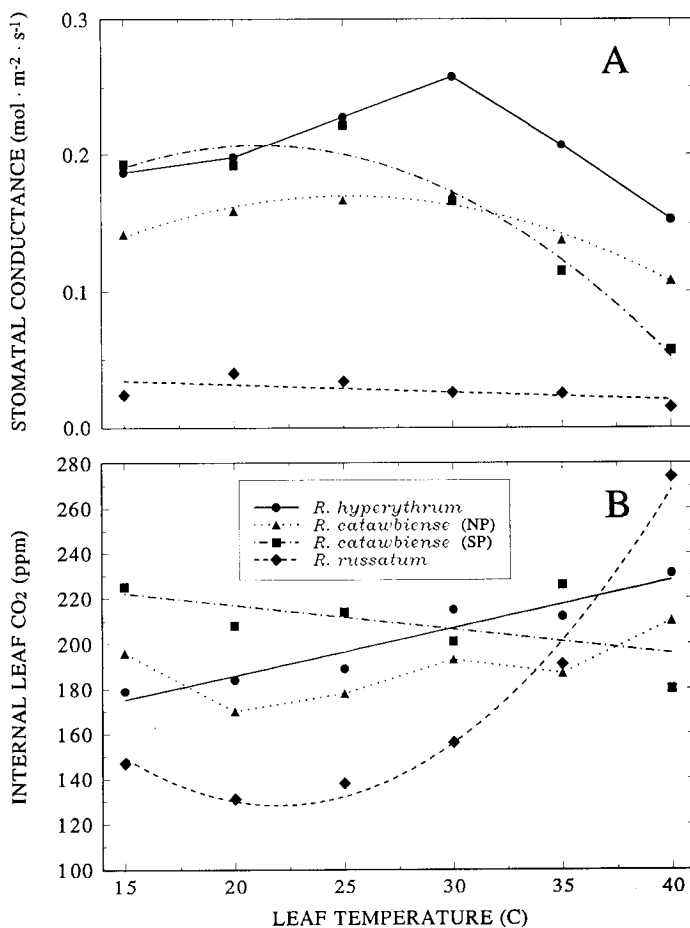
Fig. 2. Stomatal conductance (A) and calculated internal leaf CO_2 (B) of four taxa of rhododendron in response to increasing temperature. Lines represent predicted responses based on regression analyses, when significant. Symbols represent means, with n = 6. NP = northern provenance, SP = southern provenance.

Table 1. Regression equations and statistics for net photosynthesis (P_N), relative P_N, gross photosynthesis (P_G), stomatal conductance (g_s), internal leaf CO_2 concentrations (C_i), and dark respiration for Rhododendron species over a range of leaf temperatures from 15 to 40C.

	R. hyperythrum	R. catawbiense (NP)	R. catawbiense (SP)	R. russatum
P_N ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	$-5.68 + 1.71x - 0.03x^2$	$-3.67 + 1.48x - 0.03x^2$	$-2.55 + 1.34x + -0.03x^2$	$-0.67 + 0.42x - 0.01x^2$
	$P < 0.01; R^2 = 0.31$	$P < 0.01; R^2 = 0.70$	$P < 0.01; R^2 = 0.61$	$P < 0.01; R^2 = 0.48$
Relative P_N (% of max.)	$-40.17 + 10.89x - 0.22x^2$	$-24.42 + 10.31x - 0.22x^2$	$-28.09 + 11.10 - 0.24x^2$	$-416 + 58.88x - 2.13x^2 + 0.02x^3$
	$P < 0.01; R^2 = 0.78$	$P < 0.01; R^2 = 0.85$	$P < 0.01; R^2 = 0.86$	$P < 0.01; R^2 = 0.81$
P_G ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	$-5.10 + 1.65x - 0.03x^2$	$-3.21 + 1.44x - 0.03x^2$	$-2.41 + 1.33x - 0.03x^2$	$-19.02 + 2.70x - 0.10x^2 + 0.001x^3$
	$P < 0.01; R^2 = 0.97$	$P < 0.01; R^2 = 0.99$	$P < 0.01; R^2 = 0.99$	$P < 0.01; R^2 = 0.99$
g_s ($mol \cdot m^{-2} \cdot s^{-1}$)	NS	$-0.015 + 0.015x - 0.0003x^2$	$0.013 + 0.018x - 0.0004x^2$	$0.047 - 0.0007X$
		$P < 0.05; R^2 = 0.19$	$P < 0.01; R^2 = 0.41$	$P < 0.05; R^2 = 0.13$
C_i (ppm)	$143 + 2.11x$	NS	$250 - 1.73x$	$308 - 16.96x + 0.41x^2$
	$P < 0.05; R^2 = 0.16$		$P < 0.05; R^2 = 0.16$	$P < 0.01; R^2 = 0.49$
Dark respiration ($\mu mol \cdot m^{-2} \cdot s^{-1}$)	$-0.58 + 0.57x - 0.003x^2$	$-0.45 + 0.04x - 0.002x^2$	$-0.14 + 0.01x - 0.001x^2$	$-0.41 + 0.04x - 0.002x^2$
	$P < 0.01; R^2 = 0.74$	$P < 0.01; R^2 = 0.79$	$P < 0.01; R^2 = 0.89$	$P < 0.01; R^2 = 0.73$
Dark respiration[z] ($\mu mol \cdot kg^{-1} \cdot s^{-1}$)		$-1.52 + 0.15x - 0.008x^2$		
		$P < 0.01; R^2 = 0.82$		

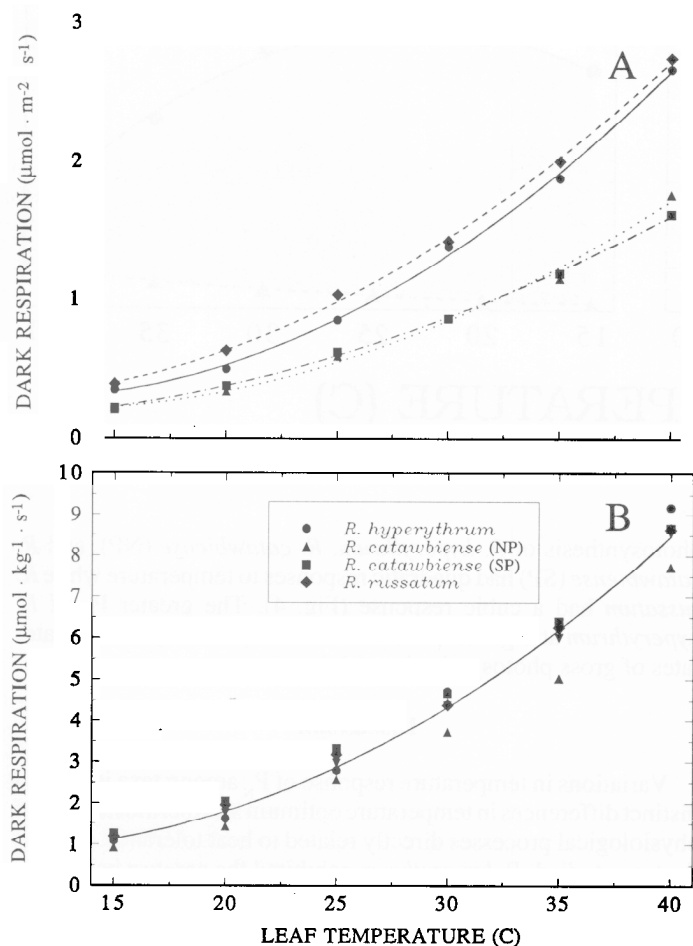[z]Main effect, pooled for all taxa.
[NS]Nonsignificant.

Fig. 3. Dark respiration rates per unit leaf area (**A**) and per unit dry weight (**B**) as a function of increasing temperature. Lines represent predicted temperature responses based on regression analyses. Symbols represent means, with n = 6. NP = northern provenance, SP = southern provenance.

Analysis of variance and regression analyses were conducted using a general linear model (PROC GLM, SAS Institute, Cary, N.C.). Main effects and comparison of means were tested at $P < 0.05$ while interactions were tested at $P < 0.10$. Simple linear or polyno-

mial curves were fit to the data when significant trends were identified in the regression analyses. Temperature optima of P_N for each plant were estimated by calculating the leaf temperature at which the first order derivative of the quadratic temperature response of P_N was equal to 0. Where $P_N = a + b$ (leaf temperature) + c (leaf temperature)^2, the temperature optimum is thereby given as $-b/(2c)$.

Results

Leaf gas exchange. A significant taxon by temperature (quadratic) interaction demonstrated that temperature responses of P_N varied by taxon. Individual regression analyses showed that P_N varied quadratically as a function of temperature for each species (Fig. 1A, Table 1). Mean calculated temperature optima for *R. hyperythrum, R. catawbiense* (NP), *R. catawbiense* (SP), and *R. russatum* were 25.2, 23.5, 22.5, and 20.0C, respectively ($LSD_{0.05} = 3.7$). Mean calculated P_N maxima (calculated from individual plant regression equations at the temperature optimum) for *R. hyperythrum, R. catawbiense* (NP), *R. catawbiense* (SP), and *R. russatum* were 15.7, 14.1, 12.6, and 3.9 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively ($LSD_{0.05} = 3.8$). At 40C, the capacity to maintain P_N varied substantially. Rates of P_N at 40C for *R. hyperthrum, R. catawbiense* (NP), *R. catawbiense* (SP), and *R. russatum* were 7.8, 5.7, 3.5, and 0.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$, respectively ($LSD_{0.05} = 1.7$).

Analysis of relative (% of maximum) P_N demonstrated a significant taxon by leaf temperature (cubic) interaction. Individual regression analyses indicated that P_N of *R. hyperythrum, R. catawbiense* (NP), and *R. catawbiense* (SP) had quadratic responses as a function of leaf temperature while *R. russatum* had a cubic response (Fig. 1B). At 40C, relative P_N rates for *R. hyperthrum, R. catawbiense* (NP), *R. catawbiense* (SP), and *R. russatum* were 51, 41, 27, and 7 (% of maximum), respectively ($LSD_{0.05} = 14$).

A significant taxon by leaf temperature (linear) interaction for g_s existed. Subsequent, independent regression analyses for each species showed temperature responses for g_s to be quadratic for the two provenances of *R. catawbiense,* a linear decrease for *R. russatum,* and no significant trend for *R. hyperythrum* (Fig. 2A). Comparisons of g_s at 40C showed a similar ranking of taxa to rankings of photosynthesis.

A significant interaction between taxon and leaf temperature (linear and quadratic) was found for calculated C_i. Subsequent, independent regression analyses for each species showed the

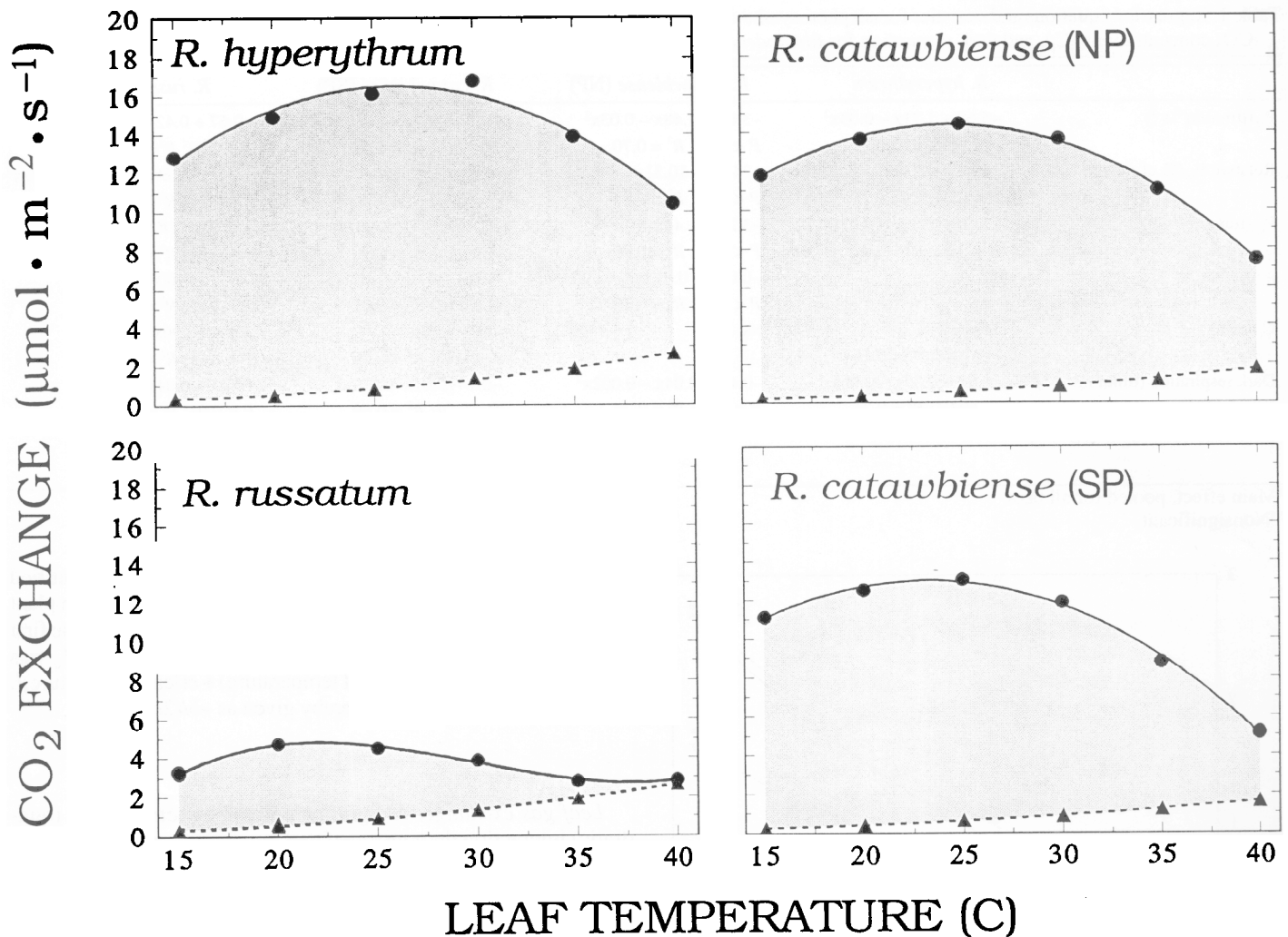J. Amer. Soc. Hort. Sci. 120(3):423–428. 1995.

425

Fig. 4. Temperature responses of gross photosynthesis (solid line), dark respiration (dotted line), and net photosynthesis (shaded area) of four taxa of rhododendron. Gross photosynthesis was approximated as the sum of net photosynthesis and dark respiration. Lines represent predicted regression responses. Symbols represent means, n =6. NP = northern provenance, SP = southern provenance.

temperature response for g_s increased linearly for *R. hyperythrurn,* decreased linearly for *R. catawbiense* (SP), exhibited a quadratic response for *R. russatum,* and had no significant trend for *R. catawbiense (NP)* (Fig. 2B). Calculated C_i for *R. hyperythrum* and the two provenances of *R. catawbiense* varied slightly with mean values ranging from 170-230 ppm among these taxa across all temperatures. In contrast, *R. russatum* had low C_i (< 160 ppm) at leaf temperatures < 30C, followed by a rapid increase in C_i to over 260 ppm at 40C.

A significant taxon by leaf temperature interaction was found for dark respiration rates when calculated on a per unit leaf area basis. Individual regression analyses showed quadratic responses for all taxa (Fig. 3A). However, when respiration rates were expressed as a function of tissue mass, there was no interaction between taxon and temperature, indicating temperature responses of respiration were similar among taxa (Fig. 3B) and that differences in respiration rates resulted primarily from variations in mass per unit leaf surface area. Further evaluation of respiration Q_s, a method for evaluating the relative change in metabolic activity as a function of temperature, showed no significant taxon or taxon by leaf temperature interaction effects on Q_s (data not presented).

Gross photosynthesis varied with an interaction between taxon and leaf temperature. Regression analyses demonstrated that gross photosynthesis of *R. hyperythrum, R. catawbiense* (NP), and *R. catawbiense* (SP) had quadratic responses to temperature while *R. russatum* had a cubic response (Fig. 4). The greater P_N of *R. hyperythrum* at high temperatures resulted primarily from greater rates of gross photosynthesis at high temperature.

Discussion

Variations in temperature response of P_N among taxa indicated distinct differences in temperature optimum and thermostability of physiological processes directly related to heat tolerance. Among the taxa studied, *R. hyperythrum* exhibited the greatest heat tolerance as indicated by a higher temperature optimum for P_N and the capacity to maintain higher Pn than any other species at 40C. In contrast, *R. russatum* had the least heat tolerance as indicated by the lowest temperature optimum for P_N and lower P_N than any other taxa at 40C. Both taxa of *R. catawbiense* were intermediate and had similar temperature optima for P_N. There was no evidence that *R. catawbiense* from the southern provenance had greater heat tolerance than plants from the northern provenance. In fact, plants from the northern provenance had greater P_N rates at 40C than plants from the southern provenance. Based on our results, ranking of these plants from greatest to least heat tolerant is given as *R. hyperythrum > [R. catawbiense* (NP) ≥ *R. catawbiense* (SP)] > *R. russatum.*

Superior heat tolerance of *R. hyperythrum* appeared to result from greater rates of gross photosynthesis, particularly in relation to dark respiration, and maintenance of high P_N rates at higher temperatures (Fig. 4). This greater photosynthetic capacity appears to be related, in part, to greater g_s. *Rhododendron hyperythrum* maintained the greatest g_s at temperatures >30C (compared to other taxa) and C_i increased with increasing temperatures which may have contributed to higher Pn. In addition, *R. hyperythrum* also appeared to have greater capacity for carbon fixation at high temperatures (40C) compared to *R. russatum* as indicated by higher P_N despite having lower C_i.

Lower heat tolerance of *R. russatum* appeared to result from several factors. Compared to other taxa, *R. russatum* had extremely low rates of gross photosynthesis (Fig. 4). As temperatures increased, gross photosynthesis decreased while dark respiration increased resulting in minimal P_N at high temperatures. However, factors limiting P_N varied with temperature. At temperatures of 30C and below, low P_N of *R. russatum* is most likely related to stomatal limitations. Over this range of temperatures, g_s of *R. russatum* ranged from only 15% to 27% of the other taxa studied. Even at the temperature optimum for R. *russatum* (i.e., 20C), *g,* was <0.05 mol·m^{-2}·s^{-1} and C_i was <140 ppm, levels that are photosynthetically limiting for most C_3 plants (Sharkey, 1985). At these lower temperatures, the low g_s of *R. russatum* apparently limited C_i which in turn limited P_N. Although the low g_s observed for *R. russatum* would tend to limit P_N, there may be other overriding evolutionary selection pressures that favor such a characteristic. *Rhododendron russatum is* an alpine plant that often grows in exposed environments, sometimes in rock crevices (Davidian, 1982a). In such environments, water conservation, regulated via limited g_s, may have evolved in response to water deficit stress, particularly in winter. Tieszen and Wieland (1975) noted that inherently low gs and low maximal P_N rates are common traits among many evergreen alpine plants including *R. lapponicum.* 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 carbohydrates at higher temperatures (Crawford and Palin, 1981; Lambers, 1985; Larcher, 1991), particularly under conditions of high night temperatures (Deal et al., 1990). At temperatures greater than 30C, g_s of *R. russatum* decreased slightly, yet C, increased rapidly, indicating that nonstomatal (e.g., metabolic, photochemical, etc.) factors became limiting. At 35C, *R. russatum* had similar C_i to other taxa, yet, P_N of *R. russatum* was only a fraction (< 13 %) of the other plants. This response indicated photosynthetic processes of *R. russatum* were also more sensitive to higher temperatures compared to the other species,

Differences in the temperature response of P_N between the two provenances of *R. catawbiense* were minor; however, plants from the southern provenance had significantly lower P_N at 40C. Greater inhibition of P_N for southern provenance plants appeared to result from a reduction in g_s that reduced C_i with increasing temperatures. Although plants in this experiment were all well-watered and vapor pressure deficits were similar at all temperatures, reduction in g_s at higher temperatures maybe an adaptation to water deficit stress that is triggered by high temperature.

Variations in heat tolerance were consistent with the native origins of these three species. *Rhododendron russatum,* an alpine species native to cool mountains, was relatively heat sensitive while *R. hyperythrum,* a native of warm climates-in Taiwan, was relatively heat tolerant. Both provenances of *R. catawbiense* were intermediate in heat tolerance. Furthermore, there was no evidence to suggest that plants of *R. catawbiense* from the southern prov-

enance offer a genetic basis for selecting or breeding superior heat tolerance in rhododendron. A similar conclusion was reached by Rowe et al. (1994a, 1994b) in evaluating. *catawbiense* from high and low elevation populations located within North Carolina. Lack of distinct differences in heat tolerance between *R. catawbiense* from different populations suggests that efforts directed at selecting and breeding rhododendron for greater heat tolerance would be better served by exploiting other species, such as *R. hyperythrum,* as a source of superior heat tolerance.

Variations in heat tolerance appeared to result from a variety of physiological factors that subsequently affected temperature optimum of P_N and the capacity for maintaining P_N at high temperatures. Although there were some differences m respiration rates among taxa at high temperature, these differences were minor in relation to differences in P_N and did not appear to be an important factor in variation in heat tolerance. Rather, the capacity for maintaining greater g_s and C_i at high temperatures was indicated as an important adaptation. This aspect of heat tolerance, however, may also vary as a function of water availability and may be less of a factor under drought y conditions. Other evidence suggested the more heat-tolerant *R. hyperythrum* maintained greater carboxylation efficiency at high temperatures, compared to *R. russatum,* as indicated by greater P_N rates despite lower C_i. Studies on heat tolerance from a variety of C_3 plants have found that reductions in P_N under high temperatures (20–40C) can result from inhibition of the water-splitting apparatus (Weis, 1982; Weis and Berry, 1987) as well as interfering with the Calvin cycle due to reduced activation of RuBP-carboxylase (Weis, 1981). Sensitivity of these photochemical and biochemical processes may also be factors in temperature sensitivity of rhododendron.

Literature Cited

Arisumi, K., E. Matsuo, Y. Sakata, and T. Tottoribe. 1986. Breeding for the heat resistant rhododendrons. Part 11 Differences of heat resistance among species and hybrids. J. Amer. Rhododendron Sot. 40:215–219.

Berry, J. and O. Bjorkman. 1980. Photosynthetic response and adaptation to temperature in higher plants. Annu. Rev. Plant Physiol,31:491–543.

Bjorkman, O., M.R. Dadger, and P.A. Armond. 1980. Response and adaptation to high temperatures, p. 233–249. In: N.C. Turner and P.J. Kramer (eds.). Adaptation of plants to water and high temperature stress. Wiley, New York.

Crawford, R.M.M. and M.A. Palin. 1981. Root respiration and temperature limits to the north-south distribution of four perennial maritime plants. Flora 171:338–354.

Davidian, H.H. 1982a. The rhododendron species. 1. Lepidotes. Timber Press, Portland, Ore.

Davidian, H.H. 1982b. The rhododendron species. III. Elepidotes. Timber Press, Portland, Ore.

Deal, D. L., J.C. Raulston, and L.E. Hinesley. 1990. Leaf color retention, dark respiration, and growth of red-leafed Japanese maples under high night temperatures. J. Amer. Soc. Hort. Sci. 115:135–140.

Fitter, A.H. and R.K.M. Hay. 1987. Environmental physiology of plants. 2nd ed. Academic Press, London.

Friend, D.J.C. and V.A. Helson. 1976. Thermoperiodic effects on the growth and photosynthesis of wheat and other crop plants. Bet. Gaz. 137:75–84.

Fryer, J.H. and F.T. Ledig. 1972. Microevolution of the photosynthetic temperature optimum in relation to the elevational complex gradient. Can J Bet. 50:1231-1235.

Hallgren, J., E. Sundbom, and M. Strand. 1982. Photosynthetic responses to low temperature in *Betula pubescens* and *Betula tortosa*. Physiol. Plant .54: 275–282.

Koike, T. and Y. Sakagami. 1985. Comparison of the photosynthetic responses to temperature and light of *Betula maximowicziana* and *Betula platyphylla* var. *japonica*. Can. J. For. Res. 15:631–635.

J. Amer. Soc. Hort. Sci. 120(3):423-428. 1995.

427

Lambers, H. 1985. Respiration in intact plants and tissues: Its regulation and dependence on environmental factors, metabolism, and invaded organisms. Encyclopedia Plant Physiol. (N.S.) 18:418-473.

Larcher, W. 1991. Physiological plant ecology. 2nd ed. Springer-Verlag, Berlin.

Leach, D.G. 1961. Rhododendrons of the world. Charles Scribners Sons, New York.

Moon, Jr, J.W, J.A. Flore, and J.F. Hancock, Jr. 1987. A comparison of carbon and water vapor gas exchange characteristics between a diploid and highbush blueberry. J. Amer. Soc. Hort. Sci. 112:134–138.

Pisek, A., W. Larcher, A. Vegis, and K. Napp-Zim. 1973. The normal temperature range, p. 102–194. In: H. Precht, J. Christopherson, H. Hensel, and W. Larcher (eds.). Temperature and life. Springer-Verlag, Berlin.

Ranney, T.G. and M.M. Peet. 1994. Heat tolerance of five taxa of birch *(Betula):* Physiological responses to supraoptimal leaf temperatures. J. Amer. Soc. Hort. Sci. 119:243-248.

Rowe, D. B., S.L. Warren, and F.A. Blazich. 1994a. Seedling growth of catawba rhododendron. I. Temperature optima, leaf area, and dry weight distribution. HortScience 29: 1298–1302.

Rowe, D. B., S.L. Warren, F.A. Blazich, and D. Mason Pharr. 1994b. Seedling growth of catawba rhododendron. II. Photosynthesis and carbohydrate accumulation and export. HortScience 29: 1303–1 308.

Sharkey, T.D. 1985. Photosynthesis in intact leaves of C3 plants: Physics, physiology and rate limitations. Bet. Rev. 51:53-105.

Slatyer, R.O. and P.J. Ferrar. 1977. Aptitudinal variation in the photosynthetic characteristics of snow gum, *Eucalyptus pauciflora* Sieb. ex Spreng. II. Effects of growth temperature under controlled conditions. Austral. J. Plant Physiol. 4:289–299.

Tesfai, M., J.W. Hanover, D.R. Layne, and J.A. Flore. 1991. Leaf temperature effects on net photosynthesis, dark respiration, and photorespiration of seedlings of black locust families with contrasting growth rates. Can. J. For. Res. 21:1616-1621.

Thornton, J.T. 1989. Growing rhododendrons in the Gulf South. J. Amer. Rhododendron Sot. 43:200-201.

Thornton, J.T. 1990. Breeding rhododendrons for the Gulf South. J. Amer. Rhododendron Soc. 44:91-93.

Tieszen, L.L and N.K. Wieland. 1975. Physiological ecology of arctic and alpine photosynthesis and respiration, p. 157-200. In: F.J. Vemberg (cd.). Physiological adaptation to the environment. Intext Educational Publ., New York.

von Caemmerer, S. and G.D. Farquhar. 1981. Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. Planta 153:376-387.

Weis, E. 1981. Reversible heat-inactivation of the Calvin cycle A possible mechanism of the temperature regulation of photosynthesis. Planta 151:33-39.

Weis, E. 1982. Influence of light on the heat sensitivity of the photosynthetic apparatus in isolated spinach chloroplasts. Plant Physiol. 70:153&1534.

Weis, E. and J.A. Berry. 1987. Quantum efficiency of photosystem II in relation to 'energy' -dependent quenching of chlorophyll fluorescence. Biochemical Biophysics Acts 894: 198–208.