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Day/Night Temperature Affects Growth and Photosynthesis of Cultivated *Salvia* Taxa

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Abstract. Eight taxa of *Salvia* L., representing broad geographic origin and diversity within the genus, were grown under long day conditions for 36 d at 15-h days of 20, 25, 30, 35, or 40 °C and 9-h nights of 15 or 25 °C. Taxa of European origin displayed broader tolerance to high day temperatures (DTs) with the lowest relative reduction in growth and net photosynthesis (P_n) occurring at DTs 30 °C or greater compared with those native to North and South America. *Salvia splendens* Sell. ex Roem. & Schult. (scarlet sage) was particularly intolerant of high temperatures with all plants dying at days of 40 °C. All plants of *S. nemorosa* L.'Ostfriesland' ('Ostfriesland' wood sage), *S. pratensis* L. (meadow sage), and *S.* × *sylvestris* L. 'Mainacht' ('May Night' salvia) survived at days of 40 °C with no visual signs of injury, whereas all other taxa except *S. splendens* exhibited stunted, contorted growth with foliar chlorosis and necrosis at 40 °C. Day temperature exerted the primary effect on top growth, root growth, and P_n of all taxa. Night temperature effects were significant for some taxa but were of less importance than day temperature.

Salvia (salvia) comprises one of the largest genera of flowering plants in the world with 900 to 950 species occurring worldwide except in Australia (Clebsch, 1997; Sytsma and Walker, 2003). As ornamental garden plants, salvias enjoy great popularity with a large number of species, hybrids, and cultivars being represented in cultivation (Armitage, 1997; Lord, 2002; Sutton, 1999). Mexican species have long been prized for their large, showy flowers ranging in color from bright reds and oranges to cobalt blues and rich purples (Compton, 1994; Matschat, 1935). The European salvias, best known from *S. officinalis* L. (common sage), the sage of culinary and herbal uses, also offer several striking ornamental species (Dweck, 2000; Sutton, 1999). Currently, the most widely grown salvia is *S. splendens*, a tender perennial species planted as an annual bedding plant (Armitage, 1997; Sutton, 1999).

Despite both the natural and garden diversity of *Salvia* taxa, limited information exists on their physiological and environmental tolerances. Beyond the extensive work conducted on *S. splendens*, little research has been conducted on other cultivated salvias (Arnold, 1998; Latimer et al., 1999; Panagiotopoulos et al., 2000; van Iersel, 1997; Wilson et al., 2003).

High temperatures can limit plant survival and growth in warm-temperate climates such as that of the southeastern United States (American Horticultural Society, 1997). Landscape plants, in particular, are subjected to extreme conditions in urban environments (Harris et al., 1999). Surprisingly, for many plant groups, including *Salvia* taxa, tolerance to high temperatures remains largely unstudied. Variations in heat tolerance among plants can be resolved by comparing temperature sensitivity of growth, basic physiological processes such as photosynthesis, and survival across a range of temperatures (Burke, 1990, 1995; Hopkins, 1999; Lambers et al., 1998; Larcher, 1994; Leegood, 1995). The potential for acclimation and tolerance to high temperatures is variable among and within species and often reflects the temperature regime of a species' native habitat (Björkman et al., 1980). Photosynthesis is one of the most heat-sensitive processes influencing plant growth (Björkman et al., 1980). The optimal temperature for photosynthesis is often correlated with the optimal temperature for plant growth, and both optima are typically reflective of the plant's native (evolutionary origin) climate (Berry and Björkman, 1980; Ranney et al., 1995). Variation in thermotolerance of photosynthesis and respiratory systems can be principle factors in differentiating growth under high temperatures.

Despite the many studies that have tested short-term, or acute, responses to very high temperatures (e.g., 45 to 55 °C), plant productivity is known to be impaired by chronic, or long-term, exposures to lower temperatures (e.g., 30 to 40 °C) (Fitter and Hay, 2002). Therefore, the objective of this research was to characterize differences in growth and photosynthetic response to supraoptimal day and night temperatures across a diverse taxonomic range of *Salvia*.

Materials and Methods

Eight *Salvia* taxa were selected to represent a cross-section of growth forms, geographic or cultivated origin, and expected physiological tolerances (Table 1). Plants were derived from the following sources: NEM and SYL—North Creek Nurseries (Landenberg, PA); CHA, GRE, GUA, and LEU—Richard Dufresne (Greensboro, NC); PRA—Chiltern Seeds (Ulverston, UK); and SPL—Buchanan's Nursery (Raleigh, NC). All plants were grown from rooted stem cuttings, except for PRA and

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Table 1. Descriptive information on *Salvia* taxa included in this study.[z]

Scientific name	Common name	Growth form in situ	Nativity	Habitat	Comments
S. chamaedryoides Cav. (CHA)[y]	Germander sage	Evergreen perennial subshrub	Mexico (Sierra Madre Orientale, south to Mexico State)	Desert-like sites, 2100–2800 m elevation	Green- and silver-leaf forms in cultivation; former is grown widely in Europe; latter is grown exclusively in the United States
S. greggii A. Gray Furman's Red (GRE)	Autumn sage	Evergreen perennial subshrub	Southwestern Texas, south to Durango and San Luis Potosi States, Mexico	Desert sites, 1500–2800 m elevation	Cultivar originated in Kerrville, TX, in 1970s
S. guaranitica St.-Hil. ex Benth. (GUA)	Blue anise sage	Herbaceous perennial	South America (southern Brazil, Paraguay, Uruguay, and northern Argentina)	Streamside forests and thickets, 450–820 m elevation	Several cultivars grown, varying in color of the corolla and calyx
S. leucantha Cav. (LEU)	Mexican bush sage	Small shrub to herbaceous perennial	East-central Mexico	Subtropical and tropical forests	Cultivated since 1846
S. nemorosa L. 'Ostfriesland' (East Friesland) (NEM)	European wood sage	Herbaceous, basal rosette-forming perennial	Eastern, central, and southern Europe, east to central Asia	Woodlands and meadows	Cultivar originated and named by German plantsman Ernst Pagles in 1955
S. pratensis L. (PRA)	Meadow sage	Herbaceous, basal rosette-forming perennial	Throughout Europe and north Africa	Meadows, in association with grasses and other forbs	Winter conditions vary from bitterly cold to mild across species' range
S. splendens Sell. ex Roem. & Schult. (SPL)	Scarlet sage	Herbaceous perennial	Brazil	Year-round warm and humid climate, 2000–3000 m elevation	Cultivated since 1822, now known worldwide as a bedding plant
S. × *sylvestris* L. 'Mainacht' (May Night) (SYL)	European wood sage	Herbaceous, basal rosette-forming perennial	Eastern, central, and southern Europe, east to central Asia and western Siberia	Woodlands and meadows	Natural hybrid of *S. nemorosa* × *S. pratensis*; cultivar selected by German plantsman Karl Foerster in 1956; 1997 Perennial Plant Association Perennial Plant of the Year

[z] Information derived from Armitage (1997), Clebsch (1997), Compton (1994), Lord (2002), and Matschat (1935).

[y] Abbreviations for taxa used in text.

SPL, which were grown from seed. Plants, at 30 to 40 d old (measured from time of inserting cuttings into rooting medium or from sowing seeds), were transplanted into 3-L black plastic containers (height, 18.5 cm; diameter, 17 cm) containing a substrate of 8 pine bark:1 sand (by vol.) amended with 1.8 $kg \cdot m^{-3}$ dolomitic limestone. At potting, 10 plants of each taxa were harvested to determine initial top and root dry weights. Plants were dried at 65 °C until plant weight remained unchanged (72 h). Initial top and root dry weights, respectively, for each taxa were: CHA = 0.35 g and 0.1 g, NEM = 0.55 g and 0.49 g, GRE = 1.54 g and 0.66 g, GUA = 0.92 g and 0.69 g, LEU = 1.42 g and 1.0 g, SYL = 0.62 g and 0.83 g, PRA = 1.10 g and 0.74 g, and SPL = 0.87 g and 1.54 g.

On 29 Sept. 1997, all plants of the eight taxa were transferred to one of five B chambers at the Southeastern Plant Environment Laboratory (North Carolina State University Phytotron) (Thomas et al., 2004). For 7 d, all plants were grown under a 15-h day/9-h night thermoperiod of 25/20 °C with a 15-h photoperiod. From 0800 to 2300 HR daily, chamber irradiance was provided by a combination of cool-white fluorescent lamps and incandescent bulbs providing a photosynthetic photon flux of 642 $\mu mol \cdot m^{-2} \cdot s^{-1}$. Plants were watered and fertilized in the morning on alternating days with a complete nutrient solution (including micronutrients) providing N, P, and K at 106, 10, and 111 $mg \cdot L^{-1}$, respectively (Thomas et al., 2004). All plants were checked in the afternoon to determine if additional water was needed to maintain adequate substrate moisture.

On 6 Oct. 1997 (day 1), plants were arranged as a 5 × 2 × 8 factorial in a randomized complete block design with eight single-plant replications. The three main factors were 5-d temperatures [DTs (20, 25, 30, 35, or 40 °C)], two night temperatures [NTs (15 or 25 °C)], provided to plants as 15-h day/9-h night thermoperiods, and eight salvia taxa. The 15 °C nights were representative of a "cool" night temperature, whereas 25 °C was considered representative of "warm" nights based on summer conditions in Raleigh, NC. Temperatures were maintained within ±0.25 °C of the set point. Plants were moved between chambers at 0800 and 2300 HR daily to maintain appropriate day/night temperatures. Plants exposed to the same day and night temperatures were also moved daily to different areas of the chamber to simulate transient mechanical perturbations. Relative humidity (RH) was greater than 70%, and CO_2 concentration averaged 350 $\mu mol \cdot m^{-3}$.

On days 23 to 25, leaf gas exchange was measured with a portable infrared gas exchange system (LI-COR 6200; LI-COR, Lincoln, NE). Photosynthetically active radiation, air and leaf temperatures, and RH inside a 0.25-L leaf chamber were measured concurrently with gas exchange for 30 s. Data were recorded from a recently matured leaf or leaves depending on taxa on each of four plants per taxa at DTs of 20, 30, or 40 °C at both NTs. Net leaf photosynthetic (P_n) rates and g_S were expressed on a leaf area basis, and leaf areas were determined using a LI-COR 3100 leaf area meter. Leaf internal CO_2 concentration (C_i) was calculated using the LI-COR 6200 software.

On day 36, plants were divided into leaves, stems, flowers (when present), and roots, and total leaf area was measured with a LI-COR 3100 leaf area meter. Leaf area of GRE was not measured as a result of the presence of glandular-tipped hairs on the leaves that adhered to the leaf area meter. Roots were placed over a screen and washed with a high-pressure water stream to remove substrate. All plant organs were dried at 65 °C until plant weight remained unchanged (72 h) and weighed. These data were used to calculate the following: top dry weight (leaf + stem dry weights), root:top ratio [RTR (root dry weight ÷ top dry weight)], and specific leaf weight [SLW (leaf dry weight ÷ leaf area)].

Data were analyzed using Proc analysis of variance in SAS (version 8.01; SAS Institute, Cary, NC). All interactions that included *Salvia* taxa were highly significant ($P \leq 0.01$) indicating all variables varied according to taxon. Therefore, data were reanalyzed by taxon as a 5 × 2 factorial. Simple linear or polynomial curves were fitted to the day temperature data when significant trends were identified in regression analyses. The maximum of the polynomial curve was calculated as a first-order derivative of the independent variable in which the dependent variable equaled zero. When appropriate, mean separations were performed through Fisher's protected least significance difference (LSD) procedure at $P = 0.05$.

Results and Discussion

Temperature affected top dry weight, stem dry weight, leaf dry weight, and leaf area similarly in all taxa and only top dry weight data are presented. Top dry weight of all *Salvia* taxa was affected by DT but not by NT (except LEU and SPL) nor the day × night temperature interaction (DT × NT) for all taxa (Table 2).

Top dry weight of all taxa responded quadratically to increasing DT with a calculated maximum top dry weight occurring at 24, 30, 22, 25, 29, 37, 33, and 26 °C for CHA, NEM, GRE, GUA, LEU, SYL, PRA, and SPL, respectively ($\text{LSD}_{0.05} = 2.1$) (Fig. 1A, B). This is the classic response to temperature with growth increasing with increasing temperature until an optimum is reached above which growth is reduced (McMichael and Burke, 1998). However, the optimal temperatures were very diverse. The three rosette-forming taxa (NEM, SYL, and PRA) exhibited the greatest tolerance to high DTs with maximum growth occurring at DTs 30 °C or greater. SYL demonstrated remarkable heat tolerance with only a minimal decline (0.7%) when comparing plants grown at 40 °C versus those at 35 °C. In contrast to *Salvia* originating from Europe (NEM, SYL, and PRA), top dry weight in New World taxa (CHA, GRE, GUA, LEU, and SPL) exhibited maximum growth at DTs 29 °C or less. Greatest top dry weights occurred at DT 25 °C or less for CHA, GRE, GUA, and DT of 26 °C for SPL. In addition, top dry weight of CHA, GRE, GUA, LEU, and SPL declined 77%, 64%, 69%, 69%, and 60% from 30 to 40 °C (35 °C for SPL), respectively. In SPL, no plants survived DTs of 40 °C. All five New World taxa exhibited stunted, contorted growth with foliar chlorosis, and necrosis at 40 °C (or 35 °C for SPL) (personal observations). The tolerance of European taxa (NEM, SYL, and PRA) to high DTs was as surprising as the lack of tolerance to high DTs of New World taxa (CHA, GRE, GUA, LEU, and SPL). In particular, SPL, which is used so commonly as a bedding plant both in Europe and North America, responded poorly to high DTs for all factors measured. Our findings with SPL agree with those of Higuchi et al. (1987) who observed strongly retarded growth in plants of *S. splendens* 'St. John's Fire' exposed to high temperatures (reaching a maximum of 45 °C) for 1 week.

For top dry weight, only LEU and SPL were significantly affected by NT (Table 2). Top dry weight of LEU increased 8% at 25 °C versus 15 °C, whereas top dry weight of SPL decreased

Table 2. Statistical significance of top and root dry weights, root:top dry weight ratio, flower dry weight, and specific leaf weight of eight *Salvia* taxa grown under contrasting day/night temperatures.

Treatment	Taxa[z]							
	CHA	NEM	GRE	GUA	LEU	SYL	PRA	SPL
				Top dry wt				
DT[y]	*	**	***	**	***	***	***	***
Linear	***	NS	*	*	NS	***	**	NS
Quadratic	***	**	***	***	***	***	***	***
NT	NS	NS	NS	NS	*	NS	NS	*
DT × NT	NS	NS	NS	NS	NS	NS	NS	NS
				Root dry wt				
DT	NS	**	***	*	***	NS	NS	*
Linear	NS	**	***	**	*	NS	NS	NS
Quadratic	NS	*	**	*	***	NS	NS	*
NT	NS	*	**	NS	NS	NS	NS	NS
DT × NT	NS	NS	NS	NS	NS	NS	NS	NS
				Root:top ratio				
DT	NS	***	NS	NS	***	***	NS	NS
Linear	NS	**	NS	NS	***	***	NS	NS
Quadratic	NS	NS	NS	NS	***	**	NS	NS
NT	NS	NS	NS	NS	*	NS	NS	NS
DT × NT	NS	NS	NS	NS	NS	NS	NS	NS
				Flower dry wt				
DT	NS	—	*	*	—	NS	—	***
Linear	NS	—	NS	**	—	NS	—	**
Quadratic	NS	—	**	***	—	NS	—	***
NT	NS	—	NS	NS	—	NS	—	NS
DT × NT	NS	—	NS	NS	—	NS	—	NS
				Specific leaf wt				
DT	***	***	—	***	***	***	*	*
Linear	NS	NS	—	NS	NS	NS	NS	NS
Quadratic	**	***	—	**	***	***	*	**
NT	*	**	—	*	***	NS	*	*
DT × NT	NS	NS	—	NS	*	NS	NS	NS

[z] CHA, NEM, GRE, GUA, LEU, SYL, PRA, and SPL represent *Salvia chamaedryoides*, *S. nemorosa* Ostfriesland, *S. greggii* Furman's Red, *S. guaranitica*, *S. leucantha*, *S.* × *sylvestris* Mainacht, *S. pratensis*, and *S. splendens*, respectively.

[y] DT, NT, and DT × NT represent day temperature (DT) and night temperature (NT) main effects, and the DT × NT interaction, respectively.

^{NS,*,**,***}Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

16% at nights of 25 °C versus nights of 15 °C (data not presented). This latter decrease may have been the result of increased dark respiration (not measured in this study) with increasing NT (Jiao and Grodzinski, 1996; Lambers et al., 1998; Leegood, 1995). Increased dry weight with increasing NT was unexpected but may relate to inherent physiological adaptations based on the native climate of the species' geographical range, resulting in a species with less physiological plasticity as observed in cultivation outside its native climatic range. (LEU, as the only taxon studied that is native to subtropical and tropical climates at low altitudes, may exhibit sensitivity to low NTs.) Contrasting results have also been found in other genera. Flowering of *Primula* ×*polyanthus* Mill. (polyantha primrose) 'Pacific Giant Dwarf Jewel Strain' was unaffected by NT (10 versus 20 °C) (Armitage and Billingsley, 1983), whereas optimum flowering of *P. vulgaris* Huds. (primrose) 'Dania Lemon Yellow' occurred at 13 °C (constant day/night temperatures) (Karlsson, 2002). This demonstrates a within-genus difference for *Primula* L. mirroring that seen for *Salvia* herein.

Root dry weight of all taxa was unaffected by DT × NT interaction (Table 2).

In contrast to top dry weight in which all taxa increased quadratically to increasing DT (Fig. 1), root dry weight responded linearly, quadratically, or was unaffected by DT depending on the taxa (Table 2). Root dry weight of NEM, GRE, and GUA declined linearly with increasing DT indicating optimal DT for root growth was 20 °C or less (Fig. 2), whereas optimal DT for top dry weight was 30, 22, and 25 °C, respectively (Fig. 1). Other studies have reported optimal DT for root growth was lower than for top growth (Jull et al., 1999; Malek et al., 1992; Rowe et al., 1994). Root dry weight of LEU and SPL increased quadratically with increasing DT with calculated maximum dry weight at DTs of 27 °C and 26 °C, respectively (Fig. 2), which was similar to optimal DTs for top dry weight of 29 °C and 26 °C, respectively (Fig. 1). Root dry weight of CHA, SYL, and PRA was unaffected by DT (data not presented). This may reflect the apparent tolerance to high DTs of SYL and PRA as exemplified by top dry weight. Only root dry weight of NEM and GRE was affected by NT decreasing 18% and 33%, respectively, at nights of 25 °C versus nights of 15 °C (Table 2, data not presented). Presumably, higher NT resulted in greater loss of respiratory carbohydrates, which reduced dry weight accumulation because temperature is the

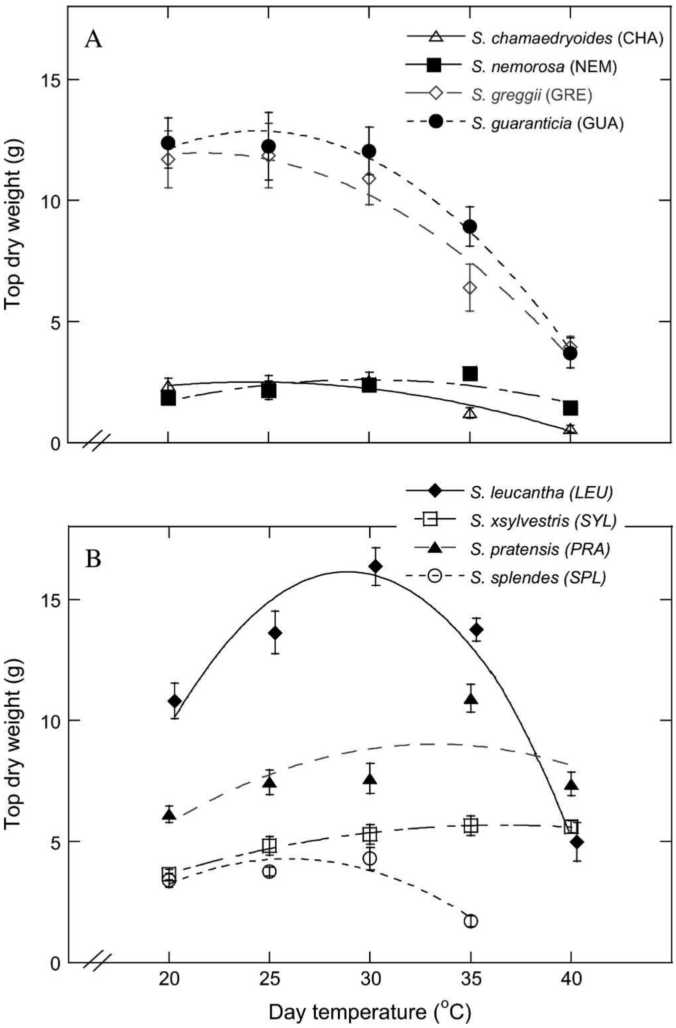

Fig. 1. Effects of day temperature on top dry weight of eight *Salvia* taxa. Symbols are means of 16 observations, vertical bars are ± 1 SE, and curves show significant quadratic effects. (**A**) S. *chamaedryoides* [CHA (top dry weight = $-2.2 + 0.39x - 0.008x^2$, $R^2 = 0.92$)], *S. nemorosa* 'Ostfriesland' [NEM (top dry weight = $-5.6 + 0.55x - 0.009x^2$, $R^2 = 0.64$)], *S. greggii* 'Furman's Red' [GRE (top dry weight = $0.15 + 1.09x - 0.025x^2$, $R^2 = 0.96$)], and *S. guaranitica* [GUA (top dry weight = $-9.58 + 1.83x - 0.038x^2$, $R^2 = 0.99$)]; (**B**) *S. leucantha* [LEU (top dry weight = $-50.5 + 4.66x - 0.081x^2$, $R^2 = 0.95$)], *S.* × *sylvestris* 'Mainacht' [SYL (top dry weight = $-4.01 + 0.53x - 0.007x^2$, $R^2 = 0.99$)], *S. pratensis* [PRA (top dry weight = $-11.5 + 1.24x - 0.019x^2$, $R^2 = 0.52$)], and *S. splendens* [SPL (top dry weight = $-15.6 + 1.53x - 0.030x^2$, $R^2 = 0.86$)].

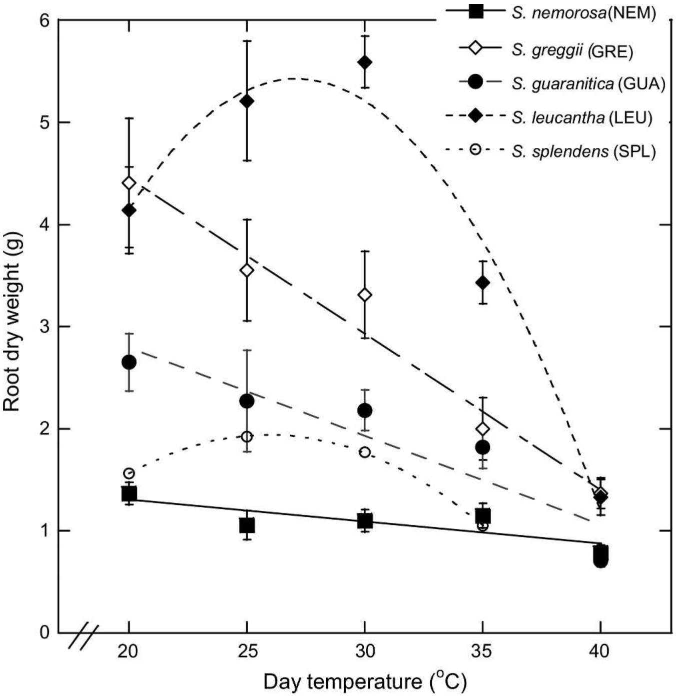

Fig. 2. Effects of day temperature on root dry weight of five *Salvia* taxa. Symbols are means of 16 observations, vertical bars are ± 1 SE, and curves show significant linear or quadratic effects. *S. nemorosa* 'Ostfriesland' [NEM (root dry weight = $1.74 + 0.02x$, $R^2 = 0.66$)], *S. greggii* 'Furman's Red' [GRE (root dry weight = $7.51 + 0.15x$, $R^2 = 0.97$)], *S. guaranitica* [GUA (root dry weight = $4.52 + 0.87x$, $R^2 = 0.85$)], *S. leucantha* [LEU (root dry weight = $-13.19 + 1.37x - 0.025x^2$, $R^2 = 0.97$)], and *S. splendens* [SPL (root dry weight = $-5.29 + 1.37x - 0.025x^2$, $R^2 = 0.97$)].

most important environmental factor influencing dark respiration (Levitt, 1980).

Top and root dry weight of LEU were inhibited by both low and high DTs with a sharp decrease (69% and 76%, respectively) from 30 to 40 °C. Although days of 20 °C are not normally considered suboptimal for most plants, LEU showed a definite spike in growth as DTs increased from 20 to 30 °C, decreasing markedly both below and above the cardinal values. Growth inhibition of LEU at low DTs may relate to suboptimal temperature conditions for adequate growth as has been reported for *S. splendens* 'Carabiniere' and 'Johannisfeuer' grown at 10 or 14 °C (Zimmer, 1980) and 'America' grown at 10 °C (Cooper and Watson, 1954). LEU was the only taxon studied native to subtropical and tropical climates at low altitudes. Thus, it may exhibit sensitivity to low DTs. In contrast, taxa native to cooler climates (CHA, NEM, GRE, GUA, and SPL) performed well at 20 °C.

Carbon allocation (RTR) was affected by DT within three taxa (Table 2). The RTR of LEU decreased linearly with increasing DT indicating root growth was more temperature-sensitive than top growth (Fig. 3). Likewise, RTR of mountain laurel (*Kalmia latifolia* L.) and catawba rhododendron (*Rhododendron catawbiense* Michx.) decreased with increasing DT (Malek et al., 1992; Rowe et al., 1994). RTR of NEM and SYL responded quadratically to increasing DT with a calculated minimum RTR occurring at 32 °C and 35 °C, respectively (Fig. 3), indicating at DTs 33 °C or greater or 36 °C or greater, respectively, top growth decreased more than root growth. Surprisingly, RTR of CHA, GRE, GUA, PRA, and SPL was unaffected by DT, NT, or DT × NT indicating growth of tops and roots responded similarly to temperature (data not presented). Jull et al. (1999) reported RTR of provenances of atlantic white cedar [*Chamaecyparis thyoides* (L.) B.S.P.] was affected by increasing DT with responses ranging from linear to quadratic to unaffected. The diversity of results may not be surprising based on Kasper and Bland (1992) who reported a decrease in RTR at both low and high DTs, whereas Cooper (1973) stated the most common response was higher RTR at low and high DTs.

Of the *Salvia* taxa studied, NEM, LEU, and PRA did not flower, either as a result of photoperiod or possibly lack of maturity or vernalization (Armitage and Laushman, 1989; Clebsch, 1997). Flower dry weight of GRE, GUA, and SPL

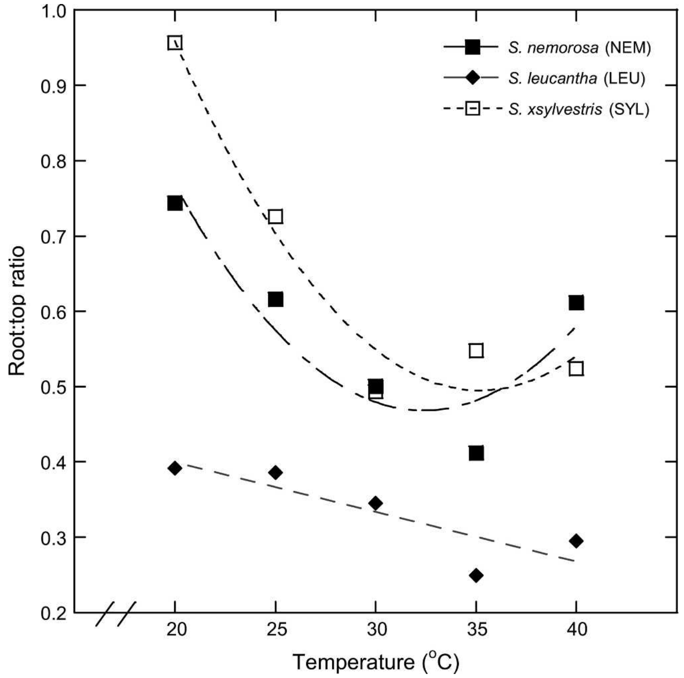

Fig. 3. Effects of day temperature on root:top ratio (RTR) of three *Salvia* taxa. Symbols are means of 16 observations, vertical bars are ± 1 SE, and curves show significant linear or quadratic effects. *S. nemorosa* 'Ostfriesland' [NEM (RTR = 2.50 + 0.126x – 0.002x^2, R^2 = 0.87)], *S. leucantha* [LEU *(RTR = 0.53 + 0.007x, R^2 = 0.73)], and *S.* ×*sylvestris* 'Mainacht' [SYL (RTR = 2.98 + 0.141x – 0.002x^2, R^2 = 0.96)].

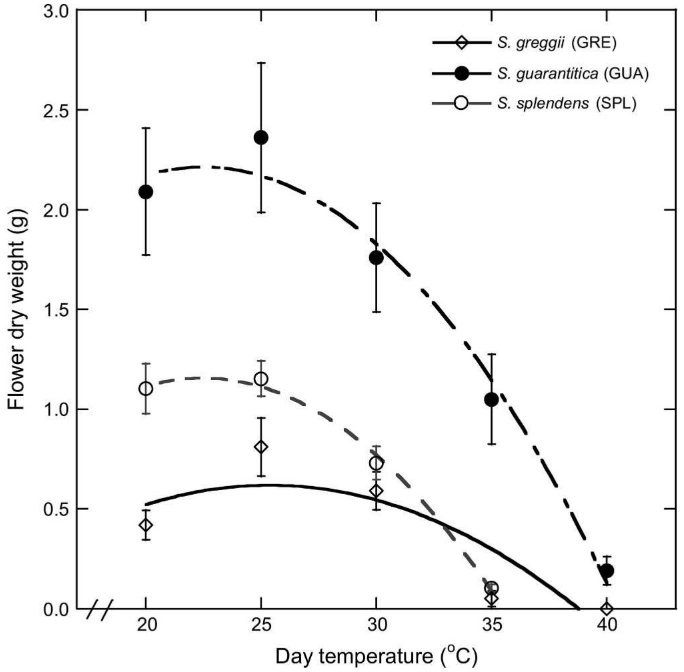

Fig. 4. Effects of day temperature on flower dry weight of three *Salvia* taxa. Symbols are means of 16 observations, vertical bars are ± 1 SE, and curves show significant quadratic effects. *S. greggii* 'Furman's Red' [GRE (flower dry weight = –1.58 + 0.174x – 0.003x^2, R^2 = 0.74)], *S. guaranitica* [GUA (flower dry weight = –1.20 + 0.304x – 0.007x^2, R^2 = 0.98)], and *S. splendens* [SPL (flower dry weight = –2.26 + 0.304x – 0.007x^2, R^2 = 0.99)].

increased quadratically with increasing DT with calculated maxima at 25, 23, and 23 °C, respectively (Fig. 4), which were similar to the optimal DTs for top dry weight (Fig. 1). Both GRE and SPL produced flowers that did not develop fully at DTs 35 °C or greater. Of these three taxa, GUA produced twice as much or more floral biomass than either GRE or SPL ($\text{LSD}_{0.05}$ = 0.2). Similar to root dry weight, flower dry weight of GRE, GUA, and SPL was unaffected by NT and DT × NT interaction (Table 2). Flower dry weight of CHA and SYL was unaffected by DT, NT, and DT × NT interaction (Table 2, data not presented).

Specific leaf weight is a morphological index that can be used as an indirect measure of leaf thickness with a high ratio generally corresponding to a thick leaf (Friend et al., 1994). Therefore, lower SLW values were regarded as indicative of low strain on plants grown in this experiment.

SLW of all *Salvia* taxa (excluding GRE in which leaf area was not measured) was significantly affected by DT (Table 2), whereas SLW was also affected by NT more than any other measured parameter. In addition, LEU had a significant DT × NT interaction. However, although SLW was significantly affected by DT, SLW was fairly stable at DTs of 20, 25, and 30 °C for New World taxa of CHA and SPL with an abrupt increase in SLW at 35 °C (Fig. 5). Likewise, SLW of GUA was similar until 40 °C, the inflection point indicating the DT at which plant growth nearly stopped. Similar to GUA, SLW of NEM and LEU were stable at DTs of 20, 25, 30, and 35 °C with SLW increasing abruptly at 40 °C (data not presented). Old World taxa (SYL and PRA) revealed a nearly steady, although significant, response of SLW to DT that corresponded with the observed, relative tolerance to high DTs in these taxa. LEU showed clear separation of plants grown at nights of 15 or 25 °C only at days of 40 °C (data not presented), with 15 °C nights producing higher SLWs compared with 25 °C NT, indicating increased leaf thickening and decreased leaf size, which may be another indicator of sensitivity to low NT. In contrast, SLW of NEM, GUA, PRA, and SPL decreased 13%, 3%, 10%, and 18%, respectively, as NT increased from 15 °C to 25 °C (data not presented) indicating increased heat strain (thicker, smaller leaves) at higher NT.

P_n of all taxa were affected by DT; however, P_n was unaffected by NT and DT × NT (data not presented). The response of P_n to DT fell into one of four categories. CHA, NEM, and SPL had similar levels of P_n at DTs of 20 and 30 °C with a subsequent decrease at 40 °C (SPL was dead at 40 °C), P_n of GRE and LEU decreased with every increase of DT with the highest P_n at 20 °C, P_n of GUA was greatest at a DT of 30 °C with significant decreases at both 20 and 40 °C, and P_n of SYL and PRA were unaffected by DT (Table 3). Jiao and Grodzinski (1996) reported P_n of *S. splendors* was reduced 55% and 80% when a leaf was exposed to 35 and 40 °C compared with maximum P_n, which was obtained at 25 °C. P_n of CHA, GRE, and GUA, which had optimal DTs for top dry weight of less than 25 °C, decreased 109%, 97%, and 109% from 30 to 40 °C, respectively, whereas P_n of NEM, LEU, SYL, and PRA, which had optimal DTs greater than 29 °C, declined 27%, 24%, 5%, and 16% from 30 to 40 °C, respectively. This is markedly similar to the top dry weight response to DT presented previously (Fig. 1). Because almost all dry weight accumulation of plants is the result of carbon fixation, P_n might be expected to be correlated with plant growth. However, P_n is not always well correlated with growth (van Iersel, 2003).

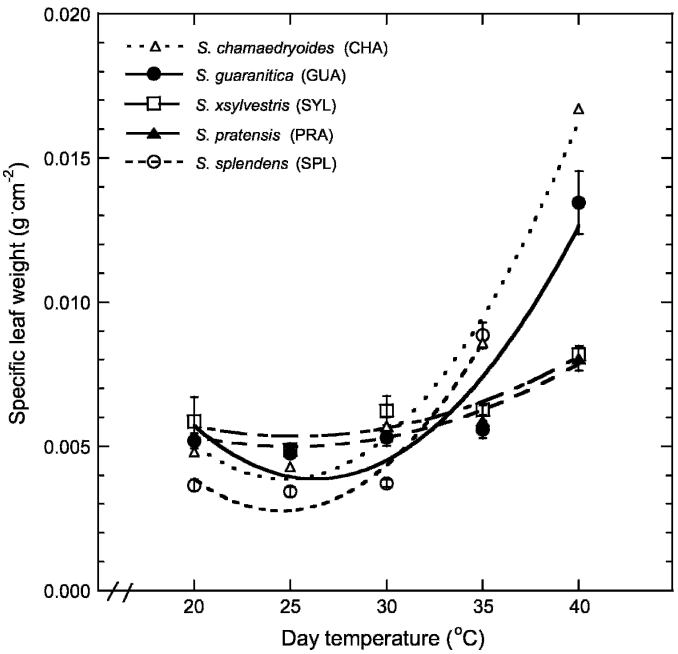

Fig. 5. Effects of day temperature on specific leaf weight of five *Salvia* taxa. Symbols are means of 16 observations, vertical bars are ± 1 SE, and curves show significant quadratic effects. *S. chamaedryoides* [CHA (specific leaf weight = $-2.2 + 0.39x - 0.008x^2$, $R^2 = 0.92$)], *S. guaranitica* [GUA (specific leaf weight = $-9.58 + 1.83x - 0.038x^2$, $R^2 = 0.99$)], *S.* × *sylvestris* 'Mainacht' [SYL (specific leaf weight = $-4.01 + 0.53x - 0.007x^2$, $R^2 = 0.99$)], *S. pratensis* [PRA (specific leaf weight = $-11.5 + 1.24x - 0.019x^2$, $R^2 = 0.52$)], and *S. splendens* [SPL (specific leaf weight = $-15.6 + 1.53x - 0.030x^2$, $R^2 = 0.86$)].

P_n of LEU illustrated the high rate of productivity that this taxon is capable of under optimum conditions (days of 20 °C). However, growth of LEU at 20 °C was dramatically reduced. Thus, high rates of P_n do not necessarily translate into high rates of growth. Although temperature effects on P_n provide a good indication how the physiological processes are affected by temperature, P_n is not always a direct indicator of plant growth, because growth is affected by photosynthesis, respiration (not measured in this study), and leaf area characteristics.

Photosynthetic measurements indicated CHA, GRE, and GUA were more sensitive to high temperatures with plants either having negative or very low P_n values at days of 40 °C. This is supported by the precipitous decrease in top dry weight at 40 °C (Fig. 1). However, what is perhaps more interesting was the unchanging values for P_n at DT of 20, 30, or 40 °C in both SYL and PRA, two highly heat-tolerant taxa. Typically, increasing temperature 10 to 15 °C above normal growth temperature leads to disorganization of chloroplast thylakoid membranes, dissociation of photosystem II light-harvesting complex, destacking of grana lamellae, separation of non-bilayer lipids of thylakoid membranes, loss of photosynthetic CO_2 evolution activity, denaturation and inactivation of many enzymes and thereby ultimately limiting photosynthesis (Dubey, 2005). The differential capacity to maintain P_n at high temperatures indicated there is considerable variation in heat tolerance or ability to acclimate to elevated temperatures among *Salvia* species.

The g_s of all taxa was affected by DT with the exception of LEU (Table 3). Lower g_s was evident at both the lowest (20 °C) and highest (40 °C) DTs for all taxa except LEU and SYL (at 25 °C NT only). Lower g_s at 20 °C was likely related to low air temperature and decreased transpiration, whereas low g_s at 40 °C may have been indicative of stomatal closure. In many instances in which stomata tend to close with increasing temperature, the closure resulted from stomatal response to an increased vapor pressure deficit, which normally results when the air temperature is increased. The leaf-to-air vapor pressure difference at elevated leaf temperature has been shown to increase stomatal closure in SPL (Jiao and Grodzinski, 1996).

The increase in g_s with increasing DT observed for SYL at NT of 25 °C was unique among the taxa studied but has been reported for several other plants (Ranney and Peet, 1994). An increase in g_s would typically result in increased transpiration and enhanced evaporative cooling, which could be an advantage at elevated temperatures (Burke and Upchurch, 1989) and would allow for greater CO_2 uptake as long as water is not limiting.

Internal leaf CO_2 concentration of GRE, GUA, and LEU increased from 30 to 40 °C, whereas C_i of CHA, NEM, and SYL was significantly equivalent between 30 and 40 °C (data not presented). Thus, although g_s decreased from DTs of 30 to 40 °C except for SYL (25 °C NT only), it appears that P_n was not CO_2-limited. In addition, C_i at 40 °C was 287 mg·L^{-1} or greater for all taxa, which should not be photosynthetically limiting for most C_3 plants (Sharkey, 1985). Increased C_i most likely resulted from increased respiration rates and decreased P_n. These data indicated inhibition of P_n at higher DTs was attributable largely to nonstomata limitations. This has been demonstrated in other herbaceous and woody perennial plants (Björkman et al., 1980; Ranney and Peet, 1994). Björkman et al. (1980) determined differences in P_n response to high temperatures was attributed to differences in the thermal stability of chloroplast components, in particular the integrity of photosystem II. Variation 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 DTs.

Maximum P_n occurred at DTs of 20 °C for GRE and LEU and up to 40 °C in SYL and PRA (Table 3). Because the 900+ species of *Salvia* span climates nearly worldwide ranging from cold temperate to tropical, the range of physiological responses should be expected to vary as observed in the present study. Of the three Old World taxa (NEM, SYL, and PRA), SYL and PRA showed no differences in P_n from 20 to 40 °C, although g_s data indicated stomatal closure or partial closure of SYL was occurring at the higher DTs (at nights of 15 °C only). In Europe, *S. nemorosa* (the wild-type equivalent of NEM) exhibited leaf temperatures ranging from 28 °C in near-pristine habitats to 37 °C in degraded habitats, yet P_n did not differ between these extremes (Nagy et al., 1994). The heat tolerance observed in situ in *S. nemorosa* may help to explain results herein for both NEM and SYL. In addition, plants from habitats with large temperature variations during the growing season tend to possess a greater potential for acclimation over a wider temperature range than plants from habitats with relatively stable temperatures during the period of active growth (Berry and Björkman, 1980). Furthermore, ecological studies with *Salvia apiana* Jepson (california white sage), a desert species native to California, exhibited P_n greater than 12 μmol·m^{-2}·s^{-1} with a leaf temperature greater than 35 °C (Schmitt et al., 1993) illustrating other *Salvia* have the capacity to maintain high P_n at elevated temperatures.

Data herein provide a foundation for response of various *Salvia* taxa to day/night temperature in broader fashion than has

Table 3. Photosynthesis and g_S of *Salvia* taxa grown under contrasting day/night temperature regimes.

	Taxa[z]							
Day temp (°C)	CHA	NEM	GRE	GUA	LEU	SYL	PRA	SPL
				Photosynthesis (μmol·m^{-2}·s^{-1})[y]				
20	1.80 a[x]	8.94 a	6.42 a	7.75 b	14.11 a	9.53 a	9.40 a	9.63 a
30	3.45 a	9.04 a	5.28 b	10.66 a	11.55 b	10.18 a	8.86 a	11.79 a
40	–0.31 b	6.57 b	0.21 c	–0.95 c	6.75 c	9.04 a	7.92 a	—
				G_S (mol·m^{-2}·s^{-1})[y]				
20	0.56 b	0.24 b	0.41 b	0.46 ab	0.45 a	—	0.34 b	0.31 b
30	0.99 a	0.62 a	0.91 a	0.61 a	0.64 a	—	0.52 a	0.66 a
40	0.38 c	0.25 b	0.31 b	0.38 b	0.41 a	—	0.32 b	—
g_S[w]				Night temp 15 °C				
20	—	—	—	—	—	0.27 c	—	—
30	—	—	—	—	—	0.93 a	—	—
40	—	—	—	—	—	0.47 b	—	—
g_S[w]				Night temp 25 °C				
20	—	—	—	—	—	0.18 c	—	—
30	—	—	—	—	—	0.40 b	—	—
40	—	—	—	—	—	0.63 a	—	—
				Taxa				
Night temp (°C)[v]	CHA	NEM	GRE	GUA	LEU	SYL	PRA	SPL
Photosynthesis	NS	*	NS	NS	***	NS	NS	NS
g_S	NS	NS	NS	NS	NS	*	***	*

[z]CHA, NEM, GRE, GUA, LEU, SYL, PRA, and SPL represent *Salvia chamaedryoides*, *S. nemorosa* Ostfriesland, *S. greggii* Furman's Red, *S. guaranitica*, *S. leucantha*, *S. × sylvestris* Mainacht, *S. pratensis*, and *S. splendens*, respectively.

[y]Day temperature × night temperature interaction not significant.

[x]Mean separation within columns per factor or per night temperature by Fisher's protected least significant difference, $P = 0.05$.

[w]Day temperature × night temperature interaction significant.

[v]Night temperature main effects analyzed separately.

[NS,*,***]Nonsignificant or significant at $P = 0.05$ or 0.001, respectively.

been reported previously. Responses of taxa of Old World origin versus those of New World origin were strikingly different. The three rosette-forming Old World taxa (NEM, SYL, and PRA) exhibited the greater tolerance to high DTs with the lowest relative reduction in growth and P_n occurring at DTs 30 °C or greater compared with New World taxa. Results of this study demonstrate that much variation in heat tolerance exists in cultivated *Salvia* that may be exploited in selection and breeding programs.

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