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 (Pn) 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 Pn of all taxa. Night temperature effects were significant for some taxa but were of less importance than day temperature.

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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; Syltman 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
Table 1. Descriptive information on *Salvia* taxa included in this study. $^z$

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


$^y$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·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 μmol·m⁻²·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 70%, and CO₂ concentration averaged 350 ppm.

Temperatures were very diverse. The three rosette-forming taxa (NEM, SYL, and PRA) 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, SYL, PRA, and SPL, respectively) increased with maximum growth occurring at DTs 29 °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, SYL, PRA, 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, GU, 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 (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, GU, LEU, and SPL) (personal observations). In 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...
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
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, 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 was unaffected by DT.
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 (LSD0.05 = 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.

Pn of all taxa were affected by DT; however, Pn was unaffected by NT and DT × NT (data not presented). The response of Pn to DT fell into one of four categories. CHA, NEM, and SPL had similar levels of Pn at DTs of 20 and 30 °C with a subsequent decrease at 40 °C (SPL was dead at 40 °C), Pn of GRE and LEU decreased with every increase of DT with the highest Pn at 20 °C, Pn of GUA was greatest at a DT of 30 °C with significant decreases at both 20 and 40 °C, and Pn of SYL and PRA were unaffected by DT (Table 3). Jiao and Grodzinski (1996) reported Pn of *S. splendors* was reduced 55% and 80% when a leaf was exposed to 35 and 40 °C compared with maximum Pn, which was obtained at 25 °C. Pn 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 Pn 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, Pn might be expected to be correlated with plant growth. However, Pn is not always well correlated with growth (van Iersel, 2003).
P<sub>n</sub> 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<sub>n</sub> do not necessarily translate into high rates of growth. Although temperature effects on P<sub>n</sub> provide a good indication of how the physiological processes are affected by temperature, P<sub>n</sub> 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<sub>n</sub> 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<sub>n</sub> 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<sub>2</sub> evolution activity, denaturation and inactivation of many enzymes and thereby ultimately limiting photosynthesis (Dubey, 2005). The differential capacity to maintain P<sub>n</sub> at high temperatures indicated there is considerable variation in heat tolerance or ability to acclimate to elevated temperatures among Salvia species.

The g<sub>s</sub> of all taxa was affected by DT with the exception of LEU (Table 3). Lower g<sub>s</sub> 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<sub>s</sub> at 20 °C was likely related to low air temperature and decreased transpiration, whereas low g<sub>s</sub> 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<sub>s</sub> 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<sub>s</sub> 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<sub>2</sub> uptake as long as water is not limiting.

Internal leaf CO<sub>2</sub> concentration of GRE, GUA, and LEU increased from 30 to 40 °C, whereas C<sub>i</sub> of CHA, NEM, and SYL was significantly equivalent between 30 and 40 °C (data not presented). Thus, although g<sub>s</sub> decreased from DTs of 30 to 40 °C except for SYL (25 °C NT only), it appears that P<sub>n</sub> was not CO<sub>2</sub>-limited. In addition, C<sub>i</sub> at 40 °C was 287 mg·L<sup>−1</sup> or greater for all taxa, which should not be photosynthetically limiting for most C<sub>3</sub> plants (Sharkey, 1985). Increased C<sub>i</sub> most likely resulted from increased respiration rates and decreased P<sub>n</sub>. These data indicated inhibition of P<sub>n</sub> at higher DTs was attributable largely to nonstomatal 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<sub>n</sub> 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<sub>n</sub> and the capacity for maintaining P<sub>n</sub> at high DTs.

Maximum P<sub>n</sub> 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<sub>n</sub> from 20 to 40 °C, although g<sub>s</sub> 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<sub>n</sub> 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<sub>n</sub> greater than 12 μmol·m<sup>−2</sup>·s<sup>−1</sup> with a leaf temperature greater than 35 °C (Schmitt et al., 1993) illustrating other Salvia have the capacity to maintain high P<sub>n</sub> at elevated temperatures.

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

Literature Cited


