

ABSTRACT

LASSEIGNE, FRANCIS TODD. Physiological Responses of Selected Taxa of *Salvia*, *Taxus*, *Cephalotaxus*, and *Syringa* to Heat and/or Flooding. (Under the direction of Drs. Frank A. Blazich and Stuart L. Warren.)

High-temperature stress impacts growth of plants in warm-temperate, continental climates. Landscape plants, in particular, are subjected to extreme conditions in urban environments, due to reflected light and retained heat from brick, concrete, or asphalt. For most ornamental plants, tolerance to high temperatures remains largely unstudied.

Two experiments were conducted to ascertain degrees of heat tolerance across a diverse taxonomic range of cultivated *Salvia* L. (salvia, sage) taxa. In the first study, eight taxa – *Salvia chamaedryoides* Cav. (germander sage), *S. greggii* A. Gray ‘Furman’s Red’ (autumn sage), *S. guaranitica* St.-Hil. ex Benth. (blue anise sage), *S. leucantha* Cav. (Mexican bush sage), *S. nemorosa* L. ‘Ostfriesland’ (East Friesland European wood sage), *S. pratensis* L. (meadow sage), *S. splendens* Sell. ex Roem. & Schult. (scarlet sage), and *S. ×sylvestris* L. ‘Mainacht’ (May Night European wood sage) – were grown under long day conditions with 15-hour days of 20, 25, 30, 35, or 40 °C and 9-hour nights of 15 or 25 °C. All taxa originating from North or South America performed poorly – *S. chamaedryoides*, *S. greggii* ‘Furman’s Red’, *S. guaranitica*, *S. leucantha*, and *S. splendens* – exhibiting severe chlorosis and growth distortions at high temperatures (35 and 40 °C). European-derived taxa – *S. nemorosa* ‘Ostfriesland’, *S. pratensis*, *S. ×sylvestris* ‘Mainacht’ maintained or increased shoot and root dry weights under high temperature treatments, and exhibited lesser or no physical symptoms of heat stress. The second study demonstrated that *S. ×sylvestris*

'Mainacht' and *S. nemorosa* 'Puszttaflamme' were better able to maintain steady rates of net photosynthesis (P_n) at high temperatures (35 and 40 °C) than *S. guaranitica* and *S. leucantha*.

In regions with hot, humid climates, a second critical limiting factor to plant growth resides in tolerance of root systems to hot, wet conditions in poorly drained, clayey soils. Two genera that are difficult to grow under these conditions are *Taxus* L. (yews) and *Syringa* L. (lilacs). A third study was conducted to determine flood and heat tolerance across a range of cultivated yews – *Taxus canadensis* Marsh. (Canadian yew), *T. ×media* Rehd. 'Brownii' ('Brownii' Anglojapanese yew), *T. ×media* 'Densiformis' ('Densiformis' Anglojapanese yew), *T. ×media* 'Taunton' ('Taunton' Anglojapanese yew), *T. wallichiana* Zucc. var. *chinensis* (Pilg.) Florin (Chinese yew) – and the related Japanese plum-yew, *Cephalotaxus harringtonia* (Knight ex Forbes) K. Koch 'Prostrata'. Despite anecdotal evidence that *Taxus* are intolerant both of heat and poor soil drainage, cultivars of *T. ×media*, especially 'Densiformis', survived a 30-day flood and grew better than the other taxa under 16-hour days/8-hour nights of 30/26 °C.

In a fourth study, three taxa of *Syringa* were tested for growth responses to flooding at 16-hour days/8-hour nights of 25/20, 30/25, or 35/30 °C: *Syringa ×hyacinthiflora* (Lemoine) Rehd. 'California Rose' (early flowering lilac), *S. ×persica* L. (Persian lilac), and *S. vulgaris* L. (common lilac). No plants survived a 10-day flood. Both *S. ×persica* and *S. ×hyacinthiflora* 'California Rose' exhibited greater growth and higher P_n and dark respiration rates in response to increasing day temperature (up to 35 °C) compared to *S. vulgaris*.

**PHYSIOLOGICAL RESPONSES OF SELECTED TAXA OF
SALVIA, TAXUS, CEPHALOTAXUS, AND SYRINGA
TO HEAT AND/OR FLOODING**

by

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Dedication

I dedicate this dissertation in memory of the late Dr. J. C. Raulston, whose life and career were tragically cut short just as I had begun to know him and learn from his vast experiences and knowledge.

Equally, I also dedicate this research in commemoration of my grandfather, the late Bernard Lasseigne, Sr., of Parks, Louisiana, who passed away before seeing me complete my long travels toward realization of this degree.

Biography

Francis Todd Lasseigne was born and raised in the small town of Thibodaux, Louisiana, parish seat of Lafourche Parish and a semi-rural community located along the slow-moving Bayou Lafourche in the French-settled area of southern Louisiana colloquially referred to as “Cajun Country.” Growing up along a small subdivision bordered on either side by fields of sugarcane, Todd gained at an early age an appreciation for the agricultural heritage of his two grandfathers, the late Bernard Lasseigne, Sr. of Parks, Louisiana and Louis Comb of Breaux Bridge, Louisiana, both former sugarcane farmers. Working alongside his father, Leonard, with his landscaping business, and gardening at home with his mother, Janet, Todd has always been in touch with the world of horticulture. The late Pat Martin of Luling, Louisiana also served as a great inspiration to Todd, exposing him to the wondrous diversity of tropical foliage plants at his garden center located less than half a mile from the mighty Mississippi River.

In 8th grade at East Thibodaux Junior High School (ETJHS), Todd was approached by a classmate to join the Future Farmers of America (FFA) Nursery/Landscape judging team. Joining with team members Todd Anderson and Todd Rodrigue, the ETJHS Nursery/Landscape judging team sailed up to the ranks of the Louisiana State FFA contest, placing second, in 1983.

In 1986, Todd was admitted to the University of Southwestern Louisiana (USL), Lafayette, Louisiana, where he began pursuit of a B.S. in Horticulture, completing the degree in 1990. His horticulture professors, Drs. Ellis Fletcher and Dennis Wollard, greatly

influenced him to complete an Honors B.S. at USL and subsequently pursue graduate studies in horticulture elsewhere. Todd left Louisiana in 1991 to pursue a Master's degree in Horticulture at the University of Georgia, Athens, Georgia, under the direction of Dr. Tim Smalley. In the midst of this degree, Todd was awarded the Martin McLaren Horticultural Scholarship, which allowed him to study abroad in the United Kingdom for 1 year – working in institutions such as the Royal Botanic Garden, Edinburgh, Scotland and the Royal Botanic Gardens, Kew, England and undertaking coursework at the University of Reading, England. This experience abroad was seminal for Todd and allowed for development of entirely new avenues of thinking about plant diversity, phytogeography, plant conservation, garden history and design, and the history of plant introduction/cultivation.

Returning to the U.S., Todd worked for one year at the State Botanical Garden of Georgia, Athens, Georgia, and then held an interluding internship for the City of Aiken, South Carolina (where he met Bob McCartney of Woodlanders Nursery, who cemented Todd's realization of the potential for growing plants in the southeastern United States). Much to the delight of Tim Smalley (and others), Todd then completed his M.S. degree in June 1996. During his nearly 5-year tenure at the University of Georgia, Todd was inspired and challenged by the great plantsman, Dr. Michael Dirr, to achieve ever increasing heights in knowledge about the world of landscape plants. While in Georgia, Todd was also introduced by his graduate school colleague, Carleton Wood, to another great American plantsman, the late Dr. J. C. Raulston of North Carolina State University.

In August 1996, Todd began work on his Ph.D. at North Carolina State University under the direction of Drs. Stu Warren and Frank Blazich. Todd was tremendously excited

and honored to be accepted into the graduate program at N.C. State University, not only where he would hone his skills as a researcher under the co-advisorship of his two major professors, but also where he could study the amazing collection of woody landscape plants assembled at the North Carolina State University Arboretum by J. C. Raulston. Tragically, J. C. was killed in an automobile accident only 4 months after Todd arrived in Raleigh, dashing any hopes of being able to learn from Raulston's voluminous knowledge, Renaissance character, and worldly experiences. It is fortunate that Todd met and befriended an earlier protégé of J. C. in the form of Tony Avent when he first moved to Raleigh. Through Tony, Todd was introduced to many of the foremost modern-day plant hunters, plantsmen, and botanical garden professionals in the southeastern United States and beyond as would have assuredly been done otherwise through J. C.

Increasingly, and especially in light of the vacuum left by J. C.'s death, Todd was drawn into the world of public speaking. From 1997 through 1999, Todd presented lectures to garden clubs, public gardens, and nursery associations, mostly within North Carolina. In 1999, this culminated in an invitation to speak for the Woody Plant Symposium at Swarthmore College, Swarthmore, Pennsylvania. Later in 1999, Todd was asked to join the Sigma Xi Honor Society on a cultural/botanical tour of Yunnan Province, China as a horticultural advisor. Through these experiences, and also through two summers of working at the JC Raulston Arboretum as a student worker, Todd was hired in 2000 as Plant Collections Manager by Dr. Bob Lyons, Director of the Arboretum. Many speaking engagements and much travel around the U.S. ensued throughout 2000, all under the duties of this exciting new position for Todd. In 2001, Todd was hired as Assistant Director of the JC

Raulston Arboretum, a faculty level position in the Department of Horticultural Science at N.C. State University, and a title that has seen him travel on a plant expedition to the nation of Georgia; present invited lectures to nurserymen in Tokyo, Japan and national plant conferences in Portland, Oregon, Atlanta, Georgia, and Charleston, South Carolina; and visit nurseries around the United States and abroad in the United Kingdom. These experiences have all come in addition to Todd's responsibilities to his Ph.D. work, delaying but not denying him from completing this all-important goal in his life. Through diligence and hard work, and with the patience, wisdom, and guidance of his Ph.D. co-advisors, Todd completed his Ph.D. in December of 2003. Throughout all these years, innumerable friends have come into Todd's life, adding and enriching all occasions and events along the way.

Family always has been and remains a vital part of Todd's life. Living so far removed from his grandparents, aunts, uncles, and cousins has been challenging, but has also brought forth an even greater appreciation of time spent on visits back home to Louisiana. His two sisters, Angela and Cherie, and their husbands, Troy and Brian, and of course his mother and father, Janet and Leonard, continue to be the foundation on which all other things rest.

“If I have seen further it is by standing on the shoulders of giants.” . . . Isaac Newton – 1675

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In my years here at N.C. State University, I have come to know many friends and colleagues, and I have in innumerable ways benefitted from the advice and guidance of the faculty of the Department of Horticultural Science. First and foremost, I must acknowledge and thank my major professors, Drs. Frank Blazich and Stu Warren. Only I and they can know of the trials, travails, and tribulations that have come in my 7+ years in pursuit of this degree. I cannot thank them enough for their patience, understanding, and continual belief in my abilities as a professional horticulturist, researcher, writer, lecturer, presenter, and human being. I could not have chosen a better “dynamic duo” of professors to guide me in this course of pursuing and completing my Ph.D. I must also thank Dr. Tom Ranney for his always intellectually stimulating conversations, thought-provoking questions, good nature, and humor. I have enjoyed traveling with him, visiting nurseries and gardens in pursuit of that always-elusive “next great plant.” To Dr. Udo Blum, I thank him for his congenial spirit, probing questions, and dedication to all facets of good and sound, biological science. I enjoyed and benefitted from time well spent in his classes in the Department of Botany.

Mr. William Reece whole-heartedly provided me with essential and expert technical assistance on all of the experiments carried out in pursuit of this degree, and always carried out oft-mundane tasks in the spirit of good fun. Mr. Juan Acedo also rendered invaluable assistance with data collection, harvesting, and other minute, detailed work related to my research. To Dr. Judy Thomas, Director of the N.C. State Phytotron, I thank her for her support of and interest in my research conducted in the Phytotron growth chambers and

greenhouses. Dr. Bill Swallow rendered his professional expertise in guiding me through statistical analyses of my data sets, and his help and congeniality is greatly appreciated. Of the other faculty with whom I have enjoyed professional contact, I thank Dr. Paul Fantz for working with me over the years, and for educating me further in matters taxonomic. My fellow graduate students have also been invaluable in helping me reach completion of this degree. In particular, I must single out Dr. Jason Griffin, Dr. Laura Jull, Mr. Richard Olsen, and Mr. Dale Witt for their timely help, friendship, wit, advice, companionship, and traveling adventures. My friend, Mr. Matt Welch, also served in a similar capacity, as well as providing for the oft-needed R&R between experiments and long-houred weeks.

Through my 3+ years at the JC Raulston Arboretum, I have also come to know and work with a great group of professional colleagues. I thank them all, and especially Dr. Bob Lyons, for allowing me to take the time needed to write this dissertation and complete all work related to this degree, all while being an employee of the Arboretum.

Lastly, it is important that I acknowledge the contributions of special friends and my family, without whose moral (and often more) support, I would not have been able to physically or mentally endure this degree. My mother and father, Leonard and Janet, have been a constant source of inspiration and love, as have my sisters, Angela and Cherie. I cannot thank them enough for their continual belief in me and encouragement of me all along the way. I must also pay tribute to my dear friends Adrienne and Jon Roethling and Sandie Zazzara, who have put up with me, particularly over the last 12 months, as I have ground down the hours and my sanity in completing this work. There can be no greater measure of friendship than that given by these three individuals to me.

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General Introduction

High-temperature stress impacts growth of plants in warm-temperate, continental climates, such as that of the southeastern United States (Amer. Hort. Soc., 1997; Raulston, 1993). Landscape plants, in particular, are subjected to extreme conditions in urban environments, due to reflected light from concrete and retained heat from brick, concrete, or asphalt (Harris et al., 1999). For most ornamental plants, tolerance to high temperatures remains largely unstudied.

Photosynthesis and growth are affected by temperature. Although for a given plant a range of temperatures exists wherein physiological activity is adjusted through acclimation processes, exposure of plants to high temperatures can result in severe, and sometimes irreversible, injury (Berry and Björkman, 1980; Burke, 1990; Fitter and Hay, 2002; Leegood, 1995; Levitt, 1980). Whether plant responses to high temperatures are studied at the enzymatic level and called “thermal kinetic windows,” or whether a whole-plant approach is taken and the term “heat tolerance” is used, clearly defined differences among plant taxa can be ascertained by comparisons of growth and basic physiological processes across a range of thermal conditions (Burke, 1990, 1995; Hopkins, 1999; Lambers et al., 1998; Larcher, 1994; Larcher et al., 1973; Leegood, 1995; Pisek et al., 1973). Traditionally, heat stress is measured in one of two ways: a) short-term exposures (measured in minutes) of a plant or organ (e.g., a leaf) of that plant to an increasing range of temperatures, usually ranging from cold or cool (0-15 °C) to very hot (e.g., 50-60 °C), to develop a temperature response curve; and b) long-term exposures (measured in days or weeks) of different plants to varying

temperature environments to evaluate both morphological and physiological effects of high temperature stress (Berry and Björkman, 1980; Lambers et al., 1998; Pisek et al., 1973).

Extreme temperatures can occur in natural environments, although their occurrence is rare. Tolerance of air temperatures of 58 °C has been reported for *Phoenix dactylifera* L. (date palm) and other desert species (Kappen, 1981; Nobel, 1988; Pisek et al., 1973). For most plants, however, temperatures above 30-35 °C can have deleterious effects on growth and basic physiological processes. Yet, plants grown under certain production systems (e.g., containerized culture in nurseries) can experience extremely high temperatures, with root media temperatures of 58 °C being reported (Newman and Davies, 1988; Ruter and Ingram, 1992). Currently, efforts to classify plant heat tolerance remain preliminary and in need of further development (Amer. Hort. Soc., 1997; Deal and Raulston, 1989; DeGaetano and Shulman, 1990).

Growth and survival of ornamental landscape plants is also strongly determined by soil conditions, especially aspects relating to soil drainage when air and root zone temperatures are high. Based on 20 years of plant evaluation field trials of thousands of taxa, Raulston (1995) concluded that the critical limiting factor to plant growth in the southeastern United States was tolerance of root systems to hot, wet conditions in poorly drained, clayey soils. Tolerance of plants to hypoxic soil conditions, or periods of flooding, ranges significantly by taxa (Crawford, 1978, 1982; Hook, 1984; Hook and Scholtens, 1978; Kozłowski, 1984, 1997; Kozłowski and Pallardy, 1997, 2002). Research into comparative flood tolerance in woody plants has focused primarily on forest tree species, as related to production for timber, with much fewer experiments being conducted on taxa of importance

to the ornamental nursery industry (Holland et al., 2003; Hook, 1984; Kozlowski, 1984; Ranney, 1994).

Therefore, the research described in this dissertation was conducted with the goal of contrasting a diverse range of taxa in response to temperature and flooding stresses. The plants selected represented herbaceous perennials, deciduous woody shrubs, and evergreen gymnosperms of economic importance to the United States nursery industry.

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Chapter 1

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

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

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Abstract. Effects of day/night temperature on photosynthesis and growth of eight taxa of *Salvia* L., representing broad geographic origin and diversity within the genus were investigated. Plants were grown under long day conditions for 30 days at 15 hour days of 20, 25, 30, 35, or 40 °C and 9 hour nights of 15 or 25 °C. Taxa of European origin displayed broader tolerance to high temperature than those native to North and South America. *Salvia splendens* Sell. ex Roem. & Schult. (scarlet sage) was 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; while 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 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 and is the largest genus in the Lamiaceae Lindl. (mint family), with 900 to 950 species occurring worldwide except in Australia (Clebsch, 1997; Sytsma and Walker, 2003). In Mexico and Central America, nearly 500 species are native, all being classified presently in *Salvia* subgenus *Calosphace* (Epling, 1939). As yet, there is no monograph of the genus, and some evidence exists to support splitting *Salvia* into several genera (Clebsch, 1997; Sytsma and Walker, 2003).

As ornamental garden plants, salvias enjoy great popularity currently, with a large number of species, hybrids, and cultivars being represented in cultivation (Armitage, 1997; Clebsch, 1997; Compton, 1987, 1994; Griffiths, 1994; Lord, 2002; Sutton, 1999). Mexican species have long been prized (most being introduced to Europe as early as the 1700s and 1800s) due to their large, showy flowers that range in color from bright reds and oranges to cobalt blues and rich purples (Armitage, 1997; Clebsch, 1997; Compton, 1994; Matschat, 1935; Sutton, 1999). The European salvias – best known from *S. officinalis* L. (common sage), the sage of culinary and herbal uses – also offer several striking ornamental species (Armitage, 1997; Clebsch, 1997; Dweck, 2000; Sutton, 1999). Currently, the most widely grown salvia is *S. splendens*, a herbaceous 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*, for which research has focused primarily on mineral nutrition, photoperiod, water relations, growth regulation, seed germination, and production, little other physiological

research has been conducted on other cultivated salvias (Armitage, 1987; Armitage and Laushman, 1989; Arnold, 1998; Cooper and Watson, 1954; Crawford, 1961a, 1961b; Eakes et al., 1991a, 1991b; Hipp et al., 1988; Latimer et al., 1999; Panagiotopoulos et al., 2000; van Iersel, 1997; Wilson et al., 2003).

High-temperature or heat stress impacts growth of most plants in warm-temperate, continental climates such as that of the southeastern United States (Amer. Hort. Soc., 1997). Landscape plants, in particular, are subjected to extreme conditions in urban environments. Reflected light from cement or brightly-colored surfaces and retained heat from brick, cement, or asphalt surfaces both contribute to increase landscape plant heat stress (Harris et al., 1999). For many plant groups, including *Salvia* taxa, tolerance to high temperatures remains largely unstudied.

Photosynthesis and growth are affected, as are all physiological processes, by temperature. Although for a given plant a range of temperatures exists wherein physiological activity is adjusted through acclimation processes, exposure of plants to extreme high temperatures for varying periods of time (depending on taxon) results in severe, and sometimes irreversible, injury (Berry and Björkman, 1980; Burke, 1990; Fitter and Hay, 2002; Leegood, 1995). Whether these responses are viewed from an enzymatic standpoint and called “thermal kinetic windows,” or whether a whole-plant approach is taken and the term “heat tolerance” is used, clearly defined differences among plant taxa can be ascertained by comparisons of growth and basic physiological processes (Burke, 1990, 1995; Hopkins, 1999; Lambers et al., 1998; Larcher, 1994; Larcher et al., 1973; Leegood, 1995; Pisek et al., 1973).

Traditionally, heat stress is measured in one of two ways: a) short-term exposures

(measured in minutes) of a plant or leaf of that plant to an increasing range of temperatures, usually ranging from cold or cool (0-15 °C) to very hot (e.g., 50-60 °C), to develop a temperature response curve; and b) long-term exposures (measured in days or weeks) of different plants to varying temperature environments (usually in controlled environment growth chambers or greenhouses) to evaluate both morphological and physiological effects of high temperature stress (Berry and Björkman, 1980; Lambers et al., 1998; Pisek et al., 1973). Despite the large number of studies that have tested short-term, or acute, responses to very high temperatures (e.g., 50-55 °C), plant productivity is known to be impaired by chronic, or long-term, exposures to much lower temperatures (e.g., 35-40 °C) (Fitter and Hay, 2002). Therefore, the objective of this research was to characterize differences in response to chronic day and night temperature across a diverse taxonomic range of *Salvia*, representing both Mexican and European derived taxa.

Materials and Methods

Eight *Salvia* taxa were selected to represent a cross-section of growth forms, expected physiological tolerances, and geographic or cultivated origin (Table 1). This selection included three rosette-forming plants (EF, MN, and PR), three subshrubs (CH, GR, and LE), and two herbaceous perennials (GU and SP). Plants were derived from the following sources: EF and MN – North Creek Nurseries (Landenberg, Penn.); CH, GR, GU, and LE – Richard Dufresne (Greensboro, N.C.); PR – Chiltern Seeds (Ulverston, United Kingdom); and SP – Buchanan’s Nursery (Raleigh, N.C.). All plants were grown from rooted stem cuttings, except for PR and SP which were grown from seed. Plants, at 30 to 40 days old (measured from time of inserting cuttings into a rooting medium or from sowing seeds), were transplanted into 3-L

containers (I.E.M. Plastics, Reidsville, N.C.), containing a medium of 8 pine bark : 1 sand (by vol.) amended with $1.8 \text{ kg}\cdot\text{m}^{-3}$ dolomitic limestone. These containers were selected to minimize pot-boundedness, that might affect growth and physiological measurements (van Iersel, 1997).

On 29 Sept. 1997 (Day 1), all plants of the eight taxa were transferred to one of five growth chambers at the Southeastern Plant Environment Laboratory (N.C. State Univ. Phytotron). For 7 days, all plants were grown under a 15/9 h day/night acclimation regime of 25/20 °C with long day conditions. On Day 8, plants were arranged as a $5\times 2\times 8$ factorial in a randomized complete block design with eight single-plant replications per temperature treatment per taxon. The three main factors were five day temperatures (20, 25, 30, 35, or 40 °C) and two night temperatures (15 or 25 °C) provided to plants as 15/9-h thermoperiods, and eight salvia taxa. The 15 °C nights were deemed representative of a “cool” night temperature; while 25 °C was considered representative of “warm” nights based on summer conditions in Raleigh, N. C. Temperatures were maintained within ± 0.25 °C of the set point. Plants were moved between chambers at 0800 and 1700 HR daily to maintain appropriate day/night temperatures. Plants exposed to the same day and night temperature were also moved daily to different areas of the chamber to simulate transient mechanical perturbations. Relative humidity was $> 70\%$, and CO_2 concentration was 300 to $400 \mu\text{mol}\cdot\text{m}^{-3}$.

From 0700 to 2200 HR daily, chamber irradiance was provided by a combination of cool-white fluorescent lamps and incandescent bulbs resulting in a photosynthetic photon flux (*PPF*) of $642 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Plants were watered and fertilized on alternating days, with a complete nutrient solution providing N, P, and K at 106, 10, and 111 $\text{mg}\cdot\text{L}^{-1}$, respectively.

(Downs and Thomas, 1991).

On Days 30-32, leaf gas exchange was measured using a LI-COR 6200 closed portable gas-exchange system (LI-COR, Lincoln, Nebr.). Photosynthetically active radiation and air and leaf temperatures, and relative humidity inside the leaf chamber were measured concurrently with gas exchange. Net leaf photosynthetic rates and stomatal conductance were calculated using the LI-COR 6200 measurements. Data were recorded from a recently matured leaf or leaves depending upon taxa on each of four plants per taxa at days of 20, 30, or 40 °C for both night temperatures using a 0.25-L chamber for 30 s. Measurements commenced immediately after CO₂ concentration decreased in the chamber. Average CO₂ concentration was 350 μmol·m⁻³.

Thirty-six days after initiating temperature treatments (Day 43), the experiment was terminated. 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. Total plant leaf area was not measured on GR due to presence of glandular-tipped hairs on the leaves that adhered to the leaf area meter. Then, all plant organs were dried at 65 °C for 72 h and weighed. The data were used to calculate the following dry weights: shoot (sum of leaf and stem) and specific leaf weight (leaf dry weight ÷ leaf area), such that higher specific leaf weight values indicated both a decrease in leaf size and an increase in leaf thickening.

Data were subjected to analysis of variance (ANOVA) procedures (SAS Inst. Inc., 1985). All interactions that included *Salvia* taxon were highly significant ($P \leq 0.01$). Therefore, the data were reanalyzed by taxon as a 5×2 factorial. Regression analysis was conducted where appropriate (SAS Inst. Inc., 1985). Simple linear or polynomial lines were

fitted to the data when significant trends were identified in the regression analysis. All regression lines presented in Figs. 1 to 5 are significant at $P \leq 0.05$. Mean separations were performed via Fisher's protected least significance difference (LSD) procedure at $P = 0.05$.

Results

Temperature treatments significantly affected growth of all *Salvia* taxa (Table 2). Although day temperature (DT) exhibited the greatest impact on plant growth, some significant effects of night temperature (NT) and the day \times night temperature interaction (DT \times NT) were also observed in select taxa.

Shoot dry weight was affected by DT in all taxa (Fig. 1). Of the eight taxa studied, LE exhibited the strongest shoot growth, with a maximum value at 30 °C (DT). For shoot dry weight, only LE was significantly affected by NT (Table 2), with an increase of 8% at 25 °C versus 15 °C (data not presented). The three rosette-forming taxa, EF, MN, and PR, exhibited the greatest tolerance to high day temperatures with decreases in growth only above 35 °C. MN showed virtually no decline (only 0.7%) when comparing plants at 40 °C versus those at 35 °C. Among EF, MN, and PR, PR exhibited the most vigorous growth, forming larger plants than either EF or MN.

In contrast to *Salvia* originating from Europe, shoot dry weight in New World taxa decreased rapidly as DT exceeded 30 °C. Highest shoot dry weights occurred at days of 20 or 25 °C for GU and GR, respectively, and days of 30 °C for CH, LE, and SP. In SP, no plants survived days at 40 °C regardless of NT. Shoot dry weight of CH was similar from 20 to 30 °C, but declined 48% and 47% between 30 to 35 °C and 35 to 40 °C, respectively. All five New World taxa exhibited stunted, contorted growth with foliar chlorosis and necrosis at 40

°C (or 35 °C for SP).

Stem dry weight and leaf dry weight data were similar to those of shoot dry weight and are not presented (Table 2). However, leaf dry weight of SP was significantly affected by NT and DT×NT. Leaf dry weight of SP at 15 °C nights increased 36% from 20 to 30 °C DT and then declined abruptly by 75% from 30 to 35 °C DT (data not presented). Leaf growth of SP at 25 °C nights, however, increased only by 18% from 20 to 30 °C days, and then declined by only 8% from 30 to 35 °C days (data not presented).

DT significantly affected root dry weight in EF, GR, GU, LE, and PR (Table 2). Root dry weight of EF, GR, and GU, declined with increasing DT; while root growth of LE and SP was optimal at days of 30 °C and 25 °C, respectively (Fig. 2). Similar to shoot dry weight data, LE showed a strong increase of 26% in root growth at days of 20 to 30 °C, but declined sharply (by 76%) at higher DTs. For MN, root dry weight was unaffected by DT. This may reflect on the apparent tolerance to high temperature in MN, as exemplified by the shoot dry weight data. Root dry weight of MN was significantly affected by both NT and DT×NT, with the 15 °C nights yielding higher root growth in all DT treatments except 20 °C. Both EF and GR showed decreases in root dry weight, 18% and 33%, respectively, at nights of 25 °C versus nights of 15 °C (Table 2, data not presented).

Of the *Salvia* taxa studied, EF, LE, and PR did not flower, either due to photoperiod, or possibly lack of maturity or vernalization (Armitage and Laushman, 1989; Clebsch, 1997). DT significantly influenced flower dry weight of GR, GU, and SP (Table 2). All three taxa exhibited a peak in flower production at days of 25 °C, with strong declines at higher DTs (Fig. 3). Both GR and SP produced flowers that did not develop fully at days of 35 °C. At

days of 40 °C, GR did not flower and all plants of SP were dead. Of these three taxa, GU produced twice as much or more floral biomass than either GR and SP. For these three *Salvia*, flower quantity (as measured by dry weight) and quality (e.g., size of flowers, inflorescences and pigment color) declined as DT increased above 30 °C. Flower dry weight was unaffected by NT and DT×NT interaction (Table 2).

In general, within taxon, decreases in leaf area occurred at similar DTs as those that induced decreases in shoot dry weight (Fig. 4). Only two taxa differed in this regard: CH, which yielded its highest leaf area at days of 25 °C versus 30 °C days for highest shoot dry weight; and GU, with its highest leaf area at 30 °C days versus days of 20 °C for its highest shoot dry weight. These inverse trends point to the complexity of taxon × DT interactions that were seen in this study. Leaf area of four taxa, CH, EF, GU, and LE, were not significantly affected by DT×NT; while three taxa, MN, PR, and SP, had significant DT×NT (Table 2). NT significantly affected LE with a 9% increase in growth at nights of 25 °C versus 15 °C nights (data not presented).

Of the taxa showing no DT×NT interactions (Table 2), LE produced the greatest total leaf area, reaching a maximum at 30 °C (Fig. 4). The three other taxa, CH, EF, and GU, peaked at 25, 35, and 30 °C, respectively. Decreases in leaf area beyond these “cardinal” temperatures were severe: 97%, 61%, 81%, and 74% for CH, EF, GU, and LE, respectively. For MN at nights of 15 °C, leaf area peaked at days of 25 °C, whereas, for MN at nights of 25 °C, leaf area peaked at days of 35 °C. Leaf area results for PR were erratic, showing a bimodal pattern. However, plants of PR grown at days/nights of 25/25 or 35/15 °C produced the highest leaf areas of all plants in the study, attesting to adaptability and vigor of this

species. For SP, leaf area peaked at days of 30 °C for both nights of 15 °C and 25 °C. Whole-plant leaf area proved to be as sensitive a measure of response to temperature as any other parameter measured.

Although leaf area data clearly showed plant responses to temperature, specific leaf weight was used to quantify changes in leaf morphology as reflected by the stunted, contorted growth that was caused by the highest DT treatments. Specific leaf weight was calculated as the amount of leaf dry weight per unit leaf area, such that higher specific leaf weight values indicate thicker/denser leaves. Therefore, lower specific leaf weight values were regarded as indicative of low stress on plants grown in this experiment.

Specific leaf weight (SLW) of all *Salvia* taxa was significantly affected by DT and NT (except for MN) (Table 2). Results for taxa, including those that had no significant DT×NT interaction – GU, MN, PR, and SP – and those with a significant DT×NT interaction – CH, EF, and LE are presented in Fig. 5.

In general, SLW was fairly stable at days of 20, 25, or 30 °C. However, SLW increased abruptly at the highest DTs, 35 and 40 °C. New World taxa, such as GU and SP, showed abrupt indications of stress at 35 and 40 °C, respectively; this inflection point indicating the temperature at which plant growth nearly ceased. Old World taxa, such as MN and PR, revealed a nearly steady, although significant, response of specific leaf weight to DT that corresponded with the observed, relative tolerance to high DTs in these taxa. Specific leaf weight data for CH showed a much steeper increase with increasing DT, starting as low as at the 25 °C days. Effects of NT on CH were much more apparent and differed from other taxa in that 15 °C nights produced lower specific leaf weight values in the mid-ranged DT

treatments. Both EF and LE showed clear separation of plants grown at nights of 15 or 25 °C only at days of 40 °C. In both taxa, 15 °C nights produced higher specific leaf weights, indicating greater leaf thickening and decreased leaf size.

Plant specific leaf weight responses to NT also varied. Although GU, PR, EF, LE, and SP showed decreases in specific leaf weight of 3%, 10%, 13%, 14%, and 18% as NT increased from 15 to 25 °C, CH exhibited a 31% increase in specific leaf weight at the higher NT (data not presented). Clearly, whereas most taxa were less stressed in the lower NT treatments, CH showed increased specific leaf weight at 25 °C, a sign of higher plant stress or a negative response to the higher NT (Fig. 5).

Photosynthesis and stomatal conductance data also revealed interesting trends among the *Salvia* taxa, with all taxa showing significant responses to DT (Table 3). Photosynthetic measurements clearly showed that CH, GR, GU, and LE (at 15 °C nights) were highly stressed at days of 40 °C, these plants either having negative or very low values. However, what is perhaps more interesting is the unchanging values for photosynthesis at days of 20, 30, or 40 °C in both MN and PR, two highly heat-tolerant taxa. As also noted previously by dry weight and leaf area data, higher photosynthesis values did not necessarily equate to optimum plant performance across all treatments – e.g., GU and SP at 30 °C days (both heat intolerant), versus MN across all DTs (a heat tolerant taxon). Photosynthesis and stomatal conductance data for LE were erratic, although photosynthesis data showed the high rate of productivity of which this taxon is capable under optimum conditions (day/nights of 20/15 °C). Stomatal conductance data showed some conflicting trends, in that lower conductances were evident at both the lowest (20 °C) and highest (40 °C) DTs for most taxa – CH, EF, GR, GU, PR, and

MN (at 15 °C NT only). Lower stomatal conductance rates at 20 °C likely relate to low air temperature and decreased transpiration whereas low stomatal conductance at 40 °C may be indicative of stomatal closure.

Discussion

Responses of *Salvia* taxa grown in this study were variable, and to some extent unexpected. The tolerance of the European taxa (EF, MN, and PR) to high DTs was as surprising as the lack of tolerance to high DTs of New World taxa (CH, GR, GU, LE, and SP). In particular, SP, which is used so commonly as a bedding plant both in Europe and North America, responded poorly to high DTs for all factors measured.

Growth inhibition of several taxa at low DTs – e.g., SP, GU, and LE – 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); ‘America’ grown at 10 °C (Cooper and Watson, 1954); and ‘Red Hot Sally’ stored at 5 or 10 °C (Kaczperski and Armitage, 1992). Relatively low optimal temperatures have also been reported for other herbaceous plants, including *Angelonia angustifolia* Benth. (narrowleaf angelon), which displayed peak photosynthetic rates between 20 and 21 °C (Miller et al., 2001), and *Pelargonium ×hortorum* L.H. Bail. ‘Pinto Violet’ (‘Pinto Violet’ geranium), *Petunia ×hybrida* Vilm.-Andr. ‘Dreams Red’ (‘Dreams Red’ petunia), *Tagetes patula* L. ‘Antigua Orange’ (‘Antigua Orange’ French marigold), and *Viola ×wittrockiana* Gams. ‘Scarlet Bronze’ (‘Scarlet Bronze’ pansy), all of which exhibited peak photosynthesis between 13 and 16 °C (van Iersel, 2003). Lower shoot dry weights for EF, LE, and MN at days/nights of 20/25 °C may also be indicative of a negative DIF response (Berghage, 1998). Increases in DIF, which

refers to the difference between day temperature and night temperature, are associated with increases in internode length in many plants whereas a negative DIF value is associated with the opposite response.

Within the *Salvia* taxa studied, growth inhibition at days of 20 °C was most pronounced in LE, as observed for shoot dry weight, root dry weight, and leaf area data (Figs. 1, 2, and 4). Although days of 20 °C are not normally considered suboptimal for most plants, LE showed a definite spike in growth at higher temperatures, declining markedly both below and above this cardinal value. This decline at the lower DT may represent limitations to net positive carbon fixation due to limited net photosynthetic rates in the presence of relatively high respiration rates (Pisek et al., 1973). Growth inhibition at lower temperatures was observed for shoot dry weight in LE, PR, and MN (Fig. 1); for root dry weight in LE, SP, and MN (15 °C nights only) (Fig. 2); for flower dry weight in GR and GU (Fig. 3); and for leaf area in LE, PR, MN, and SP (Fig. 4).

Responses to NT also varied by taxon. Although fewer significant responses to NT were seen than for DT, some interesting contrasting responses existed between taxa. In LE, which exhibited strong increases in shoot dry weight and leaf area with initial increasing temperature, higher NT resulted in significant increases in shoot dry weight (Fig. 1), stem dry weight (data not presented), and leaf area (Fig. 4). In contrast, SP declined in leaf dry weight at NTs of 25 °C versus NTs of 15 °C (data not presented). This latter decline may have been due to increased dark respiration and /or photorespiration (both not measured in this study) (Berry and Björkman, 1980; Jiao and Grodzinski, 1996; Lambers et al., 1998; Leegood, 1995; Madore and Grodzinski, 1984). Increases in dry weight with increasing NT are difficult to

explain but may relate to inherent physiological adaptations based on the native climate of the species' geographical range – in this case, resulting in a species with less physiological plasticity, as observed in cultivation outside its native climatic range. (LE, as the only taxon studied that is native to subtropical and tropical climates at low altitudes, may exhibit sensitivity to low NTs.) Crawford (1960) observed increases in respiration associated with floral induction in *S. splendens* 'St. John's Fire' (reported as 'Feu de la Saint Jean'). However, since LE is an obligate short-day plant, requiring a 10-h photoperiod to induce floral development (Armitage and Laushman, 1989), plants did not induce floral buds at any point during this study. This lack of floral induction, and subsequent lack of a floral-induction-induced increase in dark respiration (*sensu* Crawford, 1960) may explain in part the increase in growth at higher NT versus growth decreases with increasing NT in SP. Contrasting results have also been found in other genera. Armitage and Billingsley (1983) demonstrated no negative effect of night temperature (10 versus 20 °C) on flowering of *Primula* × *polyanthus* Mill. 'Pacific Giant Dwarf Jewel Strain' ('Pacific Giant Dwarf Jewel Strain' polyantha primrose); whereas Karlsson (2002) showed for *P. vulgaris* Huds. 'Dania Lemon Yellow' ('Dania Lemon Yellow' primrose) that optimum flower initiation occurred at 13 °C (constant day/night temperatures used). This demonstrates a strong within-genus difference for *Primula* L. mirroring that seen for *Salvia* herein.

Both growth and photosynthesis in all taxa were affected strongly as DT increased from 20 to 40 °C. Our findings with SP agree to some extent with those of Higuchi et al. (1987). They observed strongly retarded growth in plants of *S. splendens* 'St. John's Fire' exposed to high temperatures (6-8 °C above ambient; reaching a maximum of 45 °C) for 1

week. This growth retardation did not dissipate after 8 weeks in ambient conditions and growth cessation was overcome when plants were pruned, ultimately resulting in a greater number of lateral flowering branches. In the present study, flowering decreased strongly in SP, as well as in GR and GU.

Maximum photosynthetic rates occurred at days of 20 °C for GR and LE to up to 40 °C in MN and PR (Table 3). As the 900+ species of *Salvia* span climates nearly worldwide ranging from cold temperate to tropical, so too should the range of physiological responses be expected to vary, as we have seen in the present study. It is interesting to note that of the three Old World taxa (EF, MN, and PR), MN and PR showed no differences in photosynthesis from 20 to 40 °C; although stomatal conductance data showed that stomatal closure or partial closure of MN was occurring at the higher DTs (at nights of 15 °C only). As optimal (or statistically equivalent) photosynthetic rates were achieved for CH, EF, GU, MN, PR, and SP at days of 30 °C, this compares favorably with plants of more tropical affinity, such as the cultivated aroid *Zantedeschia* Spreng. ‘Florex Gold’ (reported as ‘Best Gold’) (‘Florex Gold’ calla-lily), which achieved maximum photosynthetic rates at 28 °C (Funnell et al., 2002).

Furthermore, ecological studies on various *Salvia* taxa have yielded valuable data. *Salvia apiana* Jepson (California white sage), a desert species native to California, exhibited net photosynthetic rates $>12 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ with a leaf temperature $> 35 \text{ }^\circ\text{C}$ (Schmitt et al., 1993). *Salvia pitcheri* Torr. ex Benth. (blue sage), a species native to the U.S. Great Plains, maintained very high photosynthetic rates ($32 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) despite low xylem pressure potential (Turner and Knapp, 1996). In Europe, *Salvia nemorosa* (the wild-type equivalent of EF) exhibited leaf temperatures ranging from 28 °C in near-pristine habitats to 37 °C in

degraded habitats; yet photosynthetic rates did not differ between these extremes (Nagy et al., 1994). The heat tolerance observed in situ in *S. nemorosa* may help to explain the results herein for both EF and MN.

In conclusion, this research provides 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. Results of this study clearly demonstrate that much variation in heat tolerance exists in cultivated *Salvia*.

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Table 1. Descriptive information on *Salvia* taxa.^z

Scientific name	Common name	Growth form <i>in situ</i>	Nativity	Habitat	Comment
<i>S. chamaedryoides</i> Cav. (CH) ^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 U.S.
<i>S. greggii</i> A. Gray 'Furman's Red' (GR)	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, Texas in 1970s
<i>S. guaranitica</i> St.- Hil. ex Benth. (GU)	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
<i>S. leucantha</i> Cav. (LE)	Mexican bush sage	Small shrub to herbaceous perennial	East central Mexico	Subtropical and tropical forests	Cultivated since 1846
<i>S. nemorosa</i> L. 'Ostfriesland' (East Friesland) (EF)	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

Table 1. (continued).

Scientific name	Common name	Growth form <i>in situ</i>	Nativity	Habitat	Comment
<i>S. pratensis</i> L. (PR)	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
<i>S. splendens</i> Sell. ex Roem. & Schult. (SP)	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
<i>S. ×sylvestris</i> L. 'Mainacht' (May Night) (MN)	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 <i>S. nemorosa</i> × <i>S. pratensis</i> ; cultivar selected by German plantsman Karl Foerster in 1956; 1997 Perennial Plant Association Perennial Plant of the Year

^zInformation derived from Armitage (1997), Clebsch (1997), Compton (1987, 1994), Epling (1939), Griffiths (1994), Lord (2002), and Matschat (1935).

^yAbbreviations for taxa used in text.

Table 2. Statistical significance of dry weight, leaf area, and specific leaf weight data of eight *Salvia* taxa grown under contrasting day/night temperatures.

Treatment	Taxa ^z							
	CH	EF	GR	GU	LE	MN	PR	SP
	<u>Shoot dry weight</u>							
DT ^y	*	**	***	**	***	***	***	***
NT	NS	NS	NS	NS	*	NS	NS	NS
DT×NT	NS	NS	NS	NS	NS	NS	NS	NS
	<u>Stem dry weight</u>							
DT	NS	*	***	***	***	*	**	*
NT	NS	NS	NS	NS	*	NS	NS	NS
DT×NT	NS	NS	NS	NS	NS	NS	NS	NS
	<u>Leaf dry weight</u>							
DT	**	**	-	**	***	**	***	***
NT	NS	NS	-	NS	NS	NS	NS	*
DT×NT	NS	NS	-	NS	NS	NS	NS	***

Table 2. (continued.)

Treatment	Taxa ^z							
	CH	EF	GR	GU	LE	MN	PR	SP
<u>Root dry weight</u>								
DT	NS	**	***	*	***	NS	*	NS
NT	NS	*	**	NS	NS	*	NS	NS
DT×NT	NS	NS	NS	NS	NS	*	NS	NS
<u>Flower dry weight</u>								
DT	NS	-	*	*	-	NS	-	***
NT	NS	-	NS	NS	-	NS	-	NS
DT×NT	NS	-	NS	NS	-	NS	-	NS
<u>Leaf area</u>								
DT	*	***	-	***	***	**	***	***
NT	NS	NS	-	NS	**	NS	*	NS
DT×NT	NS	NS	-	NS	NS	*	*	**

Table 2. (continued.)

Treatment	Taxa ^z							
	CH	EF	GR	GU	LE	MN	PR	SP
	<u>Specific leaf weight</u>							
DT	***	***	-	***	***	***	***	***
NT	*	**	-	**	***	NS	*	**
DT*NT	**	***	-	NS	***	NS	NS	NS

^z CH, EF, GR, GU, LE, MN, PR, and SP 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

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

Day temperature (° C)	Taxa ^z							
	CH	EF	GR	GU	LE	MN	PR	SP
	<u>Photosynthesis</u> ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) ^y							
20	1.80 a ^x	8.94 a	6.42 a	7.75 b	-	9.53 a	9.40 a	9.63 a
30	3.45 a	9.04 a	5.28 b	10.66 a	-	10.18 a	8.86 a	11.79 a
40	-0.31 b	6.57 b	0.21 c	-0.95 c	-	9.04 a	7.92 a	-
	<u>Stomatal conductance</u> ($\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) ^y							
20	0.56 b	0.24 b	0.41 b	0.46 ab	-	-	0.34 b	0.31 b
30	0.99 a	0.62 a	0.91 a	0.61 a	-	-	0.52 a	0.66 a
40	0.38 c	0.25 b	0.31 b	0.38 b	-	-	0.32 b	-
<u>Photosynthesis</u> ^w Night temperature 15 ° C							
20	-	-	-	-	14.73 a	-	-	-
30	-	-	-	-	11.68 b	-	-	-
40	-	-	-	-	-6.43 c	-	-	-

Table 3. Continued

Day temperature (° C)	Taxa ^z							
	CH	EF	GR	GU	LE	MN	PR	SP
<u>Photosynthesis</u> ^w Night temperature 25 ° C							
20	-	-	-	-	13.49 a	-	-	-
30	-	-	-	-	11.41 b	-	-	-
40	-	-	-	-	7.07 c	-	-	-
<u>Stomatal conductance</u> ^w Night temperature 15 ° C							
20	-	-	-	-	0.55 a	0.27 c	-	-
30	-	-	-	-	0.81 a	0.93 a	-	-
40	-	-	-	-	0.15 a	0.47 b	-	-
<u>Stomatal conductance</u> ^w Night temperature 25 ° C							
20	-	-	-	-	0.35 a	0.18 c	-	-
30	-	-	-	-	0.47 a	0.40 b	-	-
40	-	-	-	-	0.67 a	0.63 a	-	-

Table 3. Continued

Night temperature (° C) ^v	Taxa ^z							
	CH	EF	GR	GU	LE	MN	PR	SP
Photosynthesis	NS	*	NS	NS	***	NS	NS	NS
Stomatal conductance	NS	NS	NS	NS	NS	*	***	*

^z CH, EF, GR, GU, LE, MN, PR, and SP 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 measured by Fisher’s protected LSD, $P = 0.05$.

^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.

Fig. 1. Shoot dry weight of eight *Salvia* taxa in response to day temperature. Each symbol is based on 16 observations and vertical bars = ± 1 SE. (A) *S. chamaedryoides* (CH), *S. nemorosa* 'Ostfriesland' (EF), *S. greggii* 'Furman's Red' (GR), and *S. guaranitica* (GU); (B) *S. leucantha* (LE), *S. \times sylvestris* 'Mainacht' (MN), *S. pratensis* (PR), and *S. splendens* (SP).

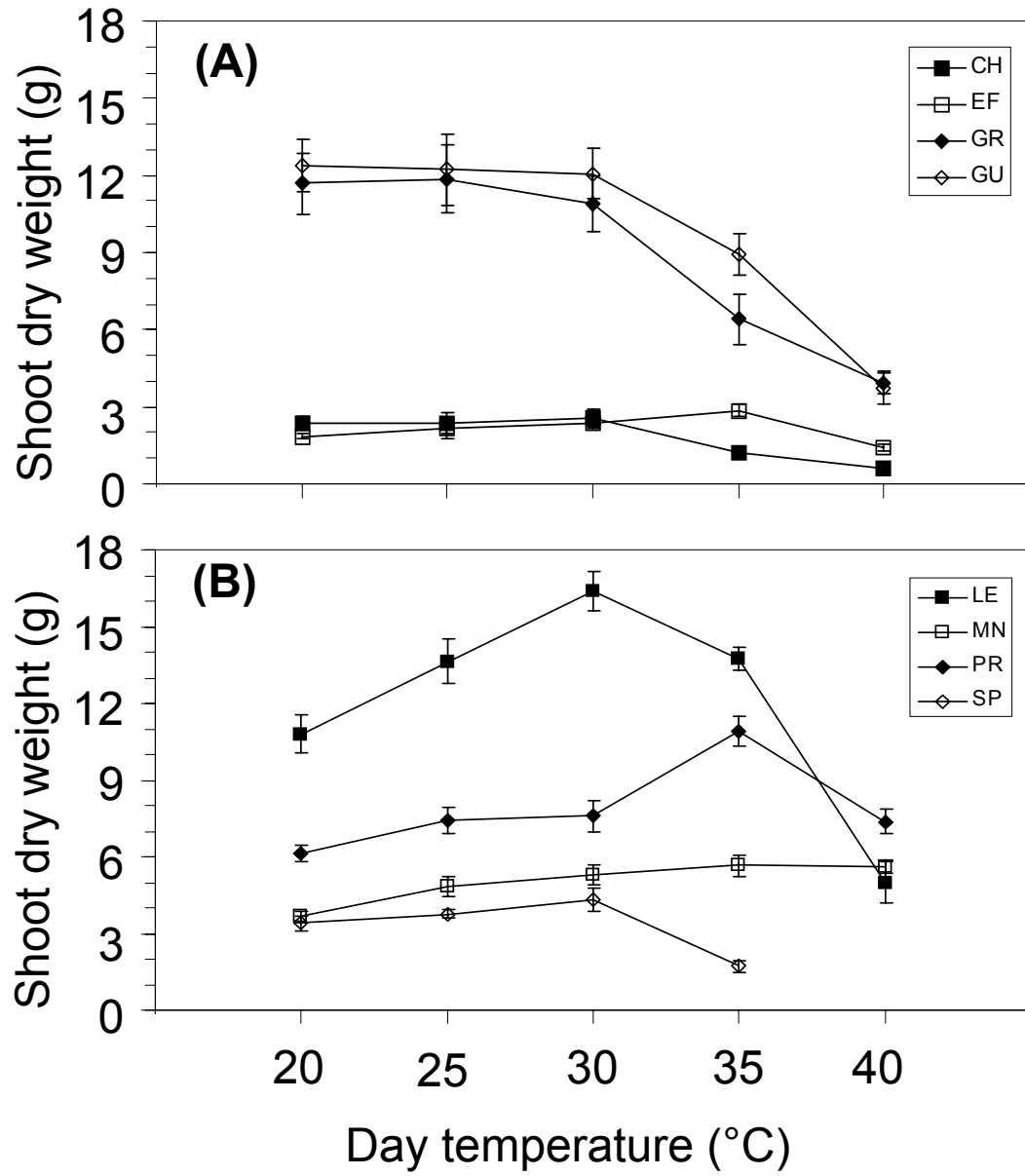


Fig. 2. Root dry weight of six *Salvia* taxa in response to (A) day temperature or (B) day/night temperature. (A) *Salvia nemorosa* ‘Ostfriesland’ (EF), *S. greggii* ‘Furman’s Red’ (GR), *S. guaranitica* (GU), *S. leucantha* (LE), and *S. splendens* (SP). Each symbol is based on 16 observations and vertical bars = ± 1 SE. (B) *S. ~~sylvestris~~* ‘Mainacht’ (MN) at nights of 15 and 25 °C due to significant DT \times NT interaction, although DT main effect not significant. Each symbol is based on 8 observations and vertical bars = ± 1 SE.

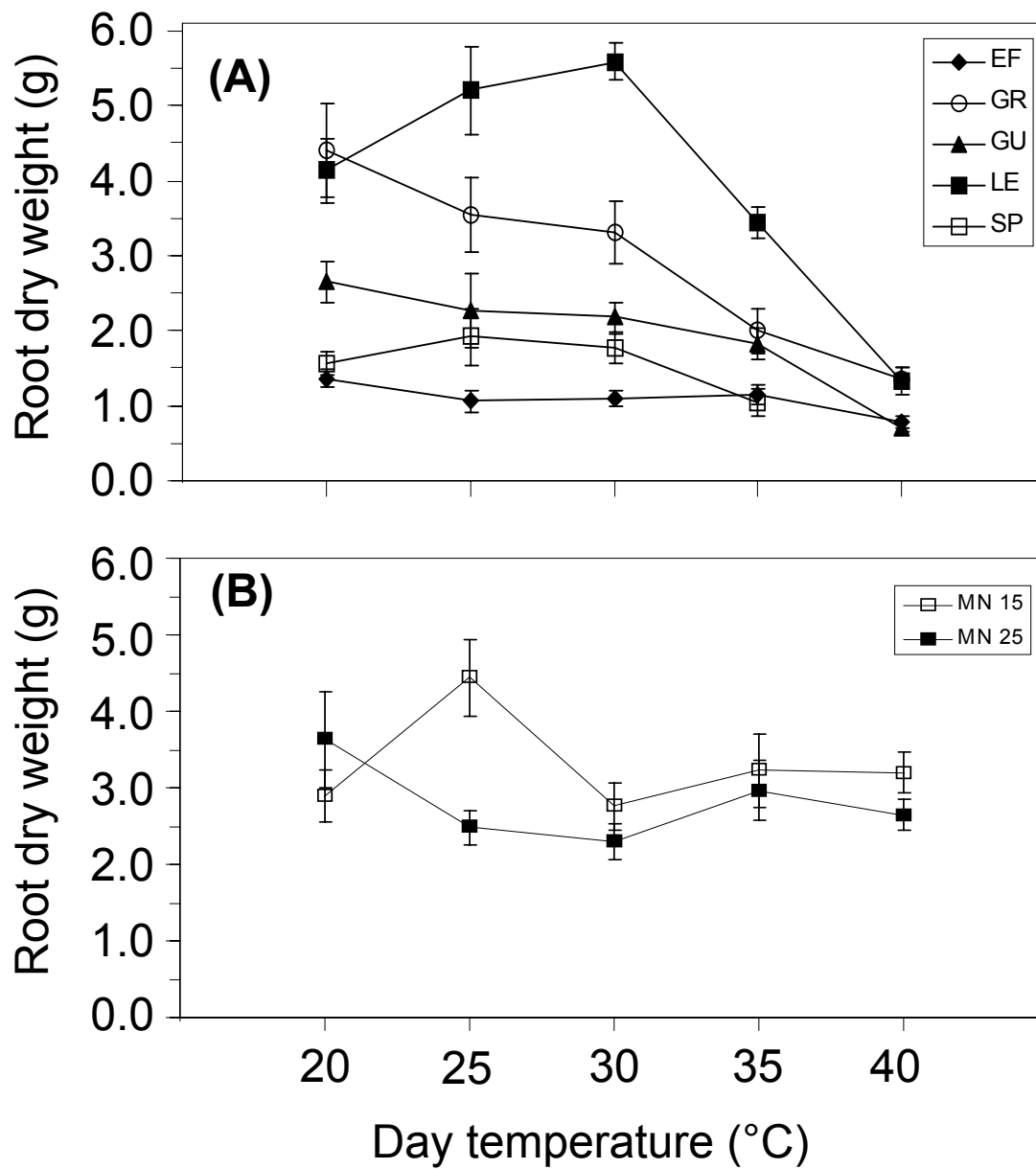


Fig. 3. Flower dry weight of *Salvia greggii* 'Furman's Red' (GR), *S. guaranitica* (GU), and *S. splendens* (SP) in response to day temperature. Each symbol is based on 16 observations and vertical bars = ± 1 SE.

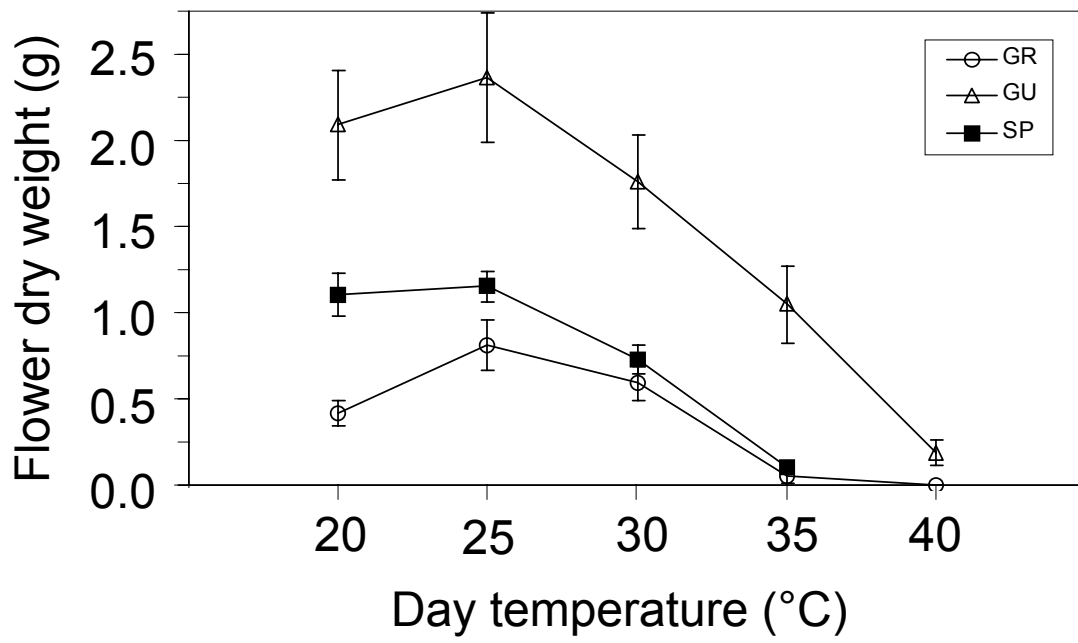


Fig. 4. Leaf area of seven *Salvia* taxa in response to day temperature or day/night temperature. (A) *Salvia chamaedryoides* (CH), *S. nemorosa* ‘Ostfriesland’ (EF), *S. guaranitica* (GU), and *S. leucantha* (LE), all with no significant day temperature (DT) × night temperature (NT) interactions. Each symbol is based on 16 observations and vertical bars = ±1 SE. (B) *S. ×sylvestris* ‘Mainacht’ (MN) at nights of 15 and 25 °C due to significant DT×NT interaction. Each symbol is based on 8 observations and vertical bars = ±1 SE. (C) *S. pratensis* (PR) at nights of 15 and 25 °C due to significant DT×NT interaction. Each symbol is based on 8 observations and vertical bars = ±1 SE. (D) *S. splendens* (SP) at nights of 15 and 25 °C due to significant DT×NT interaction. Each symbol is based on 8 observations and vertical bars = ±1 SE.

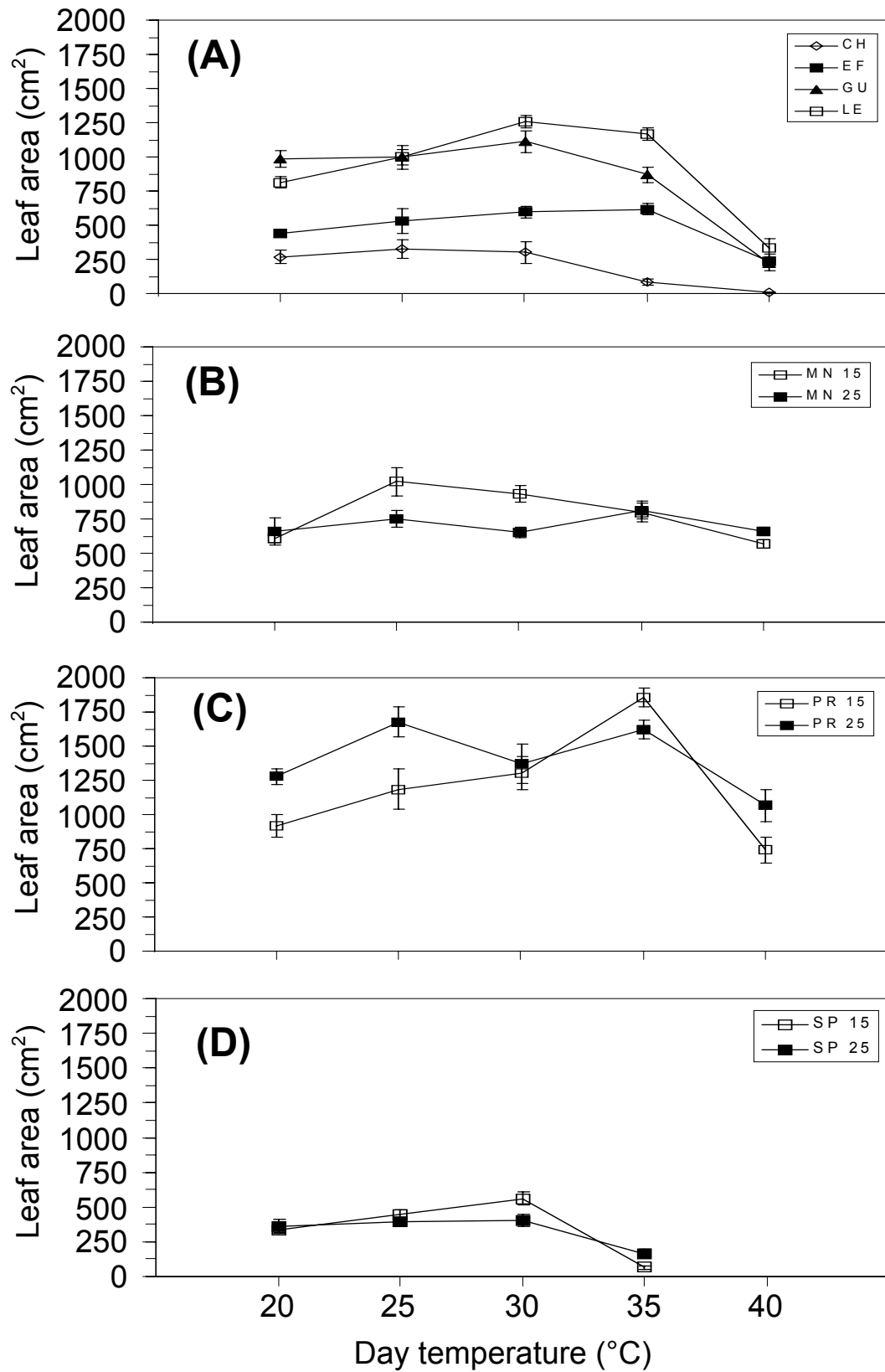


Fig. 5. Specific leaf weight of seven *Salvia* taxa in response to day temperature (DT) or day/night temperature (NT). (A) *S. guaranitica* (GU), *S. ×sylvestris* ‘Mainacht’ (MN), *S. pratensis* (PR), and *S. splendens* (SP) all with no significant DT×NT interactions. Each symbol is based on 16 observations and vertical bars = ±1 SE. (B) *S. chamaedryoides* (CH), at NTs of 15 and 25 °C due to significant DT×NT interaction. Each symbol is based on 8 observations and vertical bars = ±1 SE. (C) *S. nemorosa* ‘Ostfriesland’ (EF) at NTs of 15 and 25 °C due to significant DT×NT interaction. Each symbol is based on 8 observations and vertical bars = ±1 SE. (D) *S. leucantha* (LE) at NTs of 15 and 25 °C due to significant DT×NT interaction. Each symbol is based on 8 observations and vertical bars = ±1 SE.

