

MOISTURE STRESS CONDITIONING, POTASSIUM  
NUTRITION, AND TOLERANCE OF SALVIA SPLENDENS 'BONFIRE'  
TO MOISTURE STRESS

by

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(ABSTRACT)

The objective of this study was to determine the leaf water relations, gas exchange, and growth of the bedding plant salvia Salvia splendens 'Bonfire' as influenced by moisture stress conditioning (MSC - exposing plants to 4 sublethal dry-down cycles) and potassium (K) nutrition. Plants were fertilized with one of six K rates: 25, 75, 150, 300, 450, and 600 ppm as KCl in experiment one. Seven weeks after seeding plants were subjected to MSC. MSC and increasing K rate resulted in osmotic adjustment and increased cellular turgor potentials. Foliar K content increased as osmotic potentials decreased due to treatment. Although there was no interaction, MSC and high K rates both reduced transpiration ( $E$ ), leaf conductance ( $g_1$ ), and daily gravimetric water loss during well watered conditions. Greatest shoot dry weight occurred for plants grown with 300 ppm K and no-MSC.

Gas exchange of salvia as influenced by MSC during the onset of moisture stress was determined in experiment two. On day one follow-

ing final irrigation, MSC plants had lower mid-day  $E$ ,  $g_1$ , hourly gravimetric water loss per unit leaf area, and net photosynthesis ( $P_n$ ) compared to controls, despite no differences in leaf water potential ( $\psi_1$ ). Percentage of stomatal inhibition of  $P_n$  (SI) was greater for MSC plants than controls with no differences in mesophyllic resistance to  $CO_2$  ( $r_m$ ). On day two, MSC plants had greater  $P_n$ ,  $E$ ,  $g_1$ , and hourly gravimetric water loss per unit leaf area, while SI and  $r_m$  were lower than controls. MSC plants maintained positive  $P_n$  rates and turgor to lower  $\psi_1$  than control plants. Water use efficiency (WUE) estimates for MSC plants were greater than for controls.

Salvia plants were fertilized with 75, 300, or 600 ppm K to determine the influence of K rate on gas exchange during the onset of moisture stress in a third experiment. On day one following final irrigation, plants grown with K rates of 300 and 600 ppm had lower  $E$ ,  $g_1$ , hourly gravimetric water loss per unit leaf area, and  $P_n$  compared to 75 ppm K plants. On day two, 600 ppm K plants had greater  $P_n$ ,  $E$ , and  $g_1$  as the experiment was terminated compared to plants grown with 75 ppm K, although  $\psi_1$  was similar. Potassium rate had little affect on WUE.

## DEDICATION

This manuscript is dedicated to my wife, , our families, and my constant companion through my graduate career, . For without their patience, encouragement, support, and love, this manuscript would not have been possible.

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## Chapter I

### Introduction

Bedding plant production and use are increasing in the United States due to the high impact value of bedding plants in the landscape. Bedding plant sales have increased from \$114 million in 1977 to \$547 million in 1986 (Hamrick, 1987). This expansion in the industry will apparently continue. A survey by Bedding Plants Inc. indicated that growers intend to increase production another 11.7 percent over 1987 levels (Sallee, 1988). One major area of growth is the production in 4-inch pots of large plants that have an instant impact in the landscape (Kelly, 1987).

One of the most critical times during bedding plant production occurs when plants are removed from optimal greenhouse conditions and placed under suboptimal conditions during shipping, retail sales, and/or landscape establishment. Armitage (1986) listed post-production care as one of the five top problems facing growers today, in part due to untrained personnel entrusted with plant care, and lack of irrigation following placement in the landscape. Container plants are particularly susceptible to moisture stress due to limited root systems and soil moisture reserves. Plants may suffer from severe moisture stress under these conditions and, even if they do not die, their vigor, quality, and subsequent growth are reduced.

In the past, many growers have been mainly concerned with producing the largest plant in the least amount of time, but today many growers are beginning to recognize that their continued success

depends upon plant performance after wholesale production (Hammer, 1988). Two cultural practices that may hold promise for improving bedding plant tolerance to moisture stress are increasing potassium (K) nutrition beyond those currently used and moisture stress conditioning (MSC) during wholesale production. Consequently, the objectives of this study were to:

1. determine the influence of moisture stress conditioning and K rate on plant water relations and growth of salvia (Salvia splendens 'Bonfire');
2. examine the influence of MSC on gas exchange of salvia during moisture stress;
3. examine the influence of K rate on gas exchange of salvia during moisture stress.

### Literature Review

Current recommendations for improving post-production performance include reducing irrigation frequency, fertilizer, and greenhouse temperature during the final weeks of wholesale production. This "hardens off" plants and prepares them for suboptimal conditions including moisture stress (Armitage, 1987; Seeley, 1985). Some of these recommendations are based on work with Petunia X hybrida grown under high, normal, and low irrigation regimes through an otherwise traditional production cycle (Armitage and Kowalski, 1983). Following this production cycle, plants were watered as needed and visual evaluations and dry weight changes were determined at 5-day intervals. Plants exposed to low irrigation levels during production maintained higher

visual quality and exhibited the greatest post-production dry weight increases compared to the two higher irrigation regimes. However, none of the plants grown under any of the three moisture regimes were exposed to conditions of moisture stress, as commonly occur following production.

Tolerance to moisture stress can be accomplished by dehydration avoidance or dehydration tolerance through physiological, metabolic, and/or morphological changes (Kramer, 1983). Dehydration avoidance in higher plants is the maintenance of adequate internal moisture levels for the continuation of essential physiological and metabolic processes by reducing loss, improving absorptive capacity, or increasing storage of water. Dehydration tolerance in plants is the acclimation of these essential processes to low internal moisture levels minimizing their impact. One of the first and most important plant processes adversely affected by moisture stress is photosynthesis (Larcher, 1983). Moisture stress can limit photosynthesis by increasing stomatal diffusive resistance to  $\text{CO}_2$  during stomatal closure, reducing internal  $\text{CO}_2$  levels, or direct disruption of the photosynthetic mechanism as protoplasmic structures are damaged by reductions in internal moisture levels (Boyer, 1976; Hinkley et al., 1981).

Plant productivity depends on net photosynthesis (Pn) and photosynthate partitioning (Zelitch, 1975). Based on this, improving post-production performance of bedding plants hinges on improving cultural practices that will enhance tolerance to moisture stress through efficient water utilization and/or maintenance of Pn during potentially detrimental internal moisture levels.

### Moisture Stress Conditioning

Moisture stress conditioning (MSC), the controlled exposure of plants to moisture deficits during production, has promise as a method for improving bedding plant performance during conditions of moisture stress. Sugar maple exposed to successive periods of moisture stress followed by rehydration demonstrated less of a reduction in  $P_n$  and took less time to recover following each successive dry period than non-stressed plants (Ashton, 1956). Other authors have also reported modifications in  $P_n$  following MSC. Sunflower seedlings exposed to MSC maintained  $P_n$  rates comparable to control plants at leaf water potentials 0.3 to 0.4 MPa lower than those recorded for control plants (Matthews and Boyer, 1984). In that study, in situ and in vitro photosynthetic activity of isolated chloroplasts from MSC plants was influenced less when placed under osmotic stress compared to control plants. The authors concluded that chloroplast activity had a greater effect on photosynthetic acclimation to low leaf water potentials than stomatal function following MSC.

Seiler (1984) not only observed nonstomatal photosynthetic acclimation to low leaf water potentials in loblolly pine exposed to MSC, but also noted differences in stomatal responses to varying leaf-to-air vapor pressure deficits (VPD). Regardless of leaf water potential, MSC plants maintained lower stomatal conductance rates than control plants while VPD was high allowing MSC plants to avoid excessive water loss during situations that would usually cause high transpiration rates. Conversely, during periods of low VPD (low water loss potential) MSC plants with low leaf water potentials had greater con-

ductance rates than controls, allowing Pn to continue with a minimum of transpirational water loss. Reductions in transpirational water loss and nonstomatal inhibition of Pn during periods of adequate moisture resulted in a 67 percent increase in water use efficiency per unit leaf area ( $\mu\text{mol}$  of  $\text{CO}_2$  fixed/ $\mu\text{mol}$   $\text{H}_2\text{O}$  lost via transpiration). However, during the sublethal dry-down cycles, root and shoot dry weights were significantly reduced for MSC loblolly pine seedlings as compared to controls.

Nonstomatal inhibition of Pn during periods of low water potentials is believed to be caused by reductions in protoplast volume and, consequently, turgor (Gupta and Berkowitz, 1987). Two cultivars of wheat were exposed to a 9-day dry-down-cycle following MSC. One cultivar ('Condor') had previously displayed the ability to osmotically adjust (to actively concentrate solutes) in response to moisture stress while the second cultivar ('Capelle Desprez') lacked this capacity. Plants of 'Condor' osmotically adjusted during MSC, maintaining greater symplastic volumes and Pn rates during the 9-day stress as compared to plants of 'Capelle Desprez' which were unable to osmotically adjust during MSC. That work supports the hypothesis that nonstomatal photosynthetic acclimation to moisture stress is due to osmotic adjustment, enabling protoplasmic volume and cell turgor to be maintained.

The majority of photosynthetic acclimation observed by Gupta and Berkowitz (1987) for MSC plants was attributed to nonstomatal adaptations, but not all researchers agree. Some results suggest that stomatal changes are an important part of photosynthetic acclimation to

low leaf water potentials. Stomatal resistances for cotton seedlings receiving MSC did not increase to levels similar to those recorded for control plants until leaf water potentials for MSC plants dropped an average of 1.4 MPa below those of control plants (Brown et al., 1976). Osmotic adjustment of the abaxial guard cells for MSC plants was given as an explanation for the lower leaf water potentials required to increase stomatal resistance. Osmotic potentials of the guard cells for MSC plants were an average of 0.7 MPa lower than control plants. Similarly, maintenance of stomatal conductance during subsequent periods of moisture stress due to osmotic adjustment of the leaves has been reported for black alder exposed to MSC (Seiler, 1985). However, during the 12-week preconditioning period for these seedlings, root and shoot growth was reduced by 40 and 56 percent respectively as compared to well watered controls. Using cotton exposed to MSC, Ackerson and Hebert (1981) observed similar changes in leaf osmotic potentials and maintenance of stomatal conductance, as well as the ability to sustain  $P_n$  and translocation of photosynthates during ensuing periods of moisture stress.

Growth, and root and shoot water relations of English oak and silver birch as influenced by MSC were evaluated by Osonubi and Davies (1978). Seedlings of each species were exposed to 14 moisture stress cycles consisting of withholding water for six days followed by irrigation on the seventh. Growth parameters were evaluated for the seedlings following MSC and compared to control plants that remained well watered throughout the experiment. Height, dry weight, and leaf area of English oak were unaffected by MSC, while MSC reduced all three

growth parameters compared to controls for silver birch. The ability of English oak seedlings exposed to MSC to maintain growth during dry periods was attributed mainly to osmotic adjustment of the roots and shoots. Osonubi and Davies (1981) in a follow up study confirmed that the ability of the English oak seedlings to maintain leaf turgor, stomatal conductance, and growth during dry periods was due to osmotic adjustment of the roots and leaves. The resulting water potential gradient would favor water movement from the soil to the plant as soil water potentials drop.

MSC of swamp mahogany reduced water use by 46 percent over controls when plants were well watered without reducing shoot dry weight (Clemens and Jones, 1978). This decrease in water loss was attributed to reductions in root and shoot conductivity rather than stomatal changes because stomatal diffusive resistances for MSC plants were not different from those of control plants when both had adequate soil moisture. However, in contrast to reports of stomatal resistance being reduced by MSC during low water potentials (Ackerson and Hebert, 1981; Brown et al., 1976; Osonubi and Davies, 1978; Seiler, 1988), Clemens and Jones (1978) noted stomatal closure prior to wilt with stomatal resistance being greater for MSC plants compared to controls during water deficits.

#### Potassium Nutrition and Moisture Stress

Potassium is very important in plant water relations; while not incorporated into organic compounds K is accumulated in plant cell vacuoles and contributes to cellular osmotic potential, water uptake, and turgor. This osmoregulatory function affects many physiological

processes essential for normal plant growth including cell elongation, water retention during moisture stress, and stomatal movement (Hsiao et al.; 1976, Kramer, 1983; Mengal and Kirkby, 1982; Turner and Jones, 1980).

Water movement in and out of guard cells is regulated by vacuolar osmotic changes caused by solute accumulation, mainly  $K^+$ ,  $Cl^-$  and organic acids (Fischer, 1968). Potassium ion flux in and out of the guard cells facilitating stomatal movement is controlled by complicated interactions of environmental and internal factors (Kramer 1983; Salisbury and Ross, 1978). One of the first experiments showing a  $K^+$  requirement for stomatal opening in the presence of light used epidermal strips of broad bean. When placed in solutions of mono-valent ions, stomatal opening occurred in high concentrations of  $Li^+$ ,  $Na^+$ ,  $Cs^+$ , and  $K^+$ , but only at low  $K^+$  concentrations in the presence of light (Humble and Hsiao, 1969). Electron probe micro-analyzer studies with intact leaves of broad bean support the hypothesized role of  $K^+$  as the main ion involved in changing osmotic potential of guard cells (Fischer, 1971; Fischer and Hsiao, 1968; Humble and Raschke, 1971).

There may be a three-fold difference in  $K^+$  concentration between turgid and flaccid guard cells, with  $K^+$  originating from surrounding subsidiary cells (Fischer and Hsiao, 1968). Since guard cells comprise approximately 10 percent of the leaf epidermis, the flux of  $K^+$  required for osmoregulation and stomatal opening from any single epidermal cell is small (Fischer, 1971; Sawhney and Zelitch, 1969). Anion movement during  $K^+$  influx has been reported during stomatal opening, but in quantities insufficient to balance the charge produced by  $K^+$

influx (Fischer and Hsiao, 1968; Humble and Raschke, 1971; Humble and Hsiao, 1969). Therefore, catabolism of guard cell organic acids has been proposed to explain the charge balance required within the guard cells to maintain neutrality during  $K^+$  influx, and may also be the means for  $K^+$  transport into the guard cell (Fischer, 1971; Humble and Raschke, 1971; Meidner and Willmer, 1975). Speculation is that as malate is formed,  $H^+$  is released and  $K^+$  is taken up by the guard cells. This hypothesis is supported by both malate and  $K^+$  accumulation in guard cells during light-induced stomatal opening (Meidner and Willmer, 1975).

As previously mentioned, under normal moisture conditions stomatal closure may be controlled by a variety of interacting mechanisms. However, under stress conditions, production of abscisic acid (ABA) can cause stomatal closure (Meidner and Willmer, 1975; Salisbury and Ross, 1978). Malate formation and  $K^+$  uptake by the guard cells are prevented by ABA-induced plasma membrane changes (Salisbury and Ross, 1978). Potassium ion flux in and out of guard cells is not yet totally understood, and as more work is performed some of these hypotheses may change or become better understood.

The influence of K nutrition on stomatal aperture, transpiration, and photosynthetic rates have varied. Potassium-deficient corn plants exhibited transpiration rates 30 percent less than plants grown with high K rates, without showing visual deficiency symptoms (Koch and Estes, 1975). However, K-deficient plants also had a 70 percent reduction in  $CO_2$  uptake resulting in a 30 percent drop in dry matter yield compared to plants grown with high K nutrition rates. Similar

results were observed by Peaslee and Moss (1968) using the same species grown in sand culture and fertilized with a K-deficient solution. Rao and Rao (1983) found increased transpiration rates as K rate increased for pigeon pea grown in sand culture.

In contrast, fertilizing previously K-deficient Sitka spruce seedlings with increasing K levels led to reduced transpiration rates over a two week period (Bradbury and Malcolm, 1977). In this instance dry matter yield was not reduced and WUE increased for plants receiving high rates of K. There was also a positive correlation between stomatal resistance and leaf-to-air VPD. This stomatal sensitivity to environmental conditions conducive to high evaporative water loss could prevent excessive water loss, improving dehydration avoidance.

Wheat and pea had reduced stomatal apertures and transpiration rates at high K fertilization regimes (Brag, 1972). Increased foliar  $K^+$  concentrations observed in the study were believed to increase the osmotic potentials of subsidiary cells enough to exert pressure on the guard cells, compressing stomata and reducing transpiration. Sunflower seedlings grown under high K levels maintained a higher turgor pressure under moisture stress conditions than plants with inadequate K fertilization (Lindhauer, 1985). Under well watered conditions, plants grown with high K fertilization had lower stomatal conductance rates than K-deficient plants. However, under low water potentials, high K plants maintained higher stomatal conductance than K-deficient plants. These stomatal changes to high K rates would allow the seedlings to avoid dehydration and ultimately tolerate dehydration.

Low foliar  $K^+$  concentrations have also been shown to reduce Pn in several species (Bottrill, et al., 1970; Morard, 1974; Spencer and Possingham, 1960; Tanaka and Hara, 1974). Inhibition of Pn in K-deficient corn was suggested to be stomatal in nature (Estes et al., 1973; Koch and Estes, 1975) while reductions in Pn for K-deficient sugar beet involved both stomatal and nonstomatal factors (Terry and Ulrich, 1973).

The role of K in preventing nonstomatal inhibition of Pn may be linked to several physiological and metabolic processes. With two different species, Longstreth and Nobel (1980) and Terry and Ulrich (1973) showed that low foliar  $K^+$  concentrations reduced mesophyll cell wall permeability in the stomatal cavity to  $CO_2$  diffusion, causing nonstomatal inhibition of Pn. Lack of foliar K has increased nonstomatal inhibition of Pn in alfalfa through reductions in de novo synthesis of RuBP carboxylase, the primary enzyme involved in the Calvin cycle of carbon fixation (Peoples and Koch, 1979).

Using leaf slices of K-deficient spinach, Berkowitz and Whalen (1985) found that nonstomatal inhibition of Pn increased as moisture stress increased. Nonstomatal inhibition of Pn was increased in control plants by 14 percent as leaf slices were moved to sorbitol solutions with more negative osmotic potentials while leaf slices of K-deficient plants decreased 41 percent. Increasing foliar K insulated Pn from adverse effects of dropping leaf water potentials in intact plants (Pier and Berkowitz, 1987). Wheat seedlings irrigated with different K solutions had maximum Pn rates at high leaf water potentials when grown with 1 and 2 millimolar solutions of K. However, as

leaf water potentials decreased, Pn for seedlings grown using solutions of 6 millimolar K concentrations were 28 percent greater than those for 2 millimolar K grown seedlings.

Potassium also has a direct effect on translocation and mobilization of carbohydrates in plants (Mengal and Kirkby, 1982). Potassium ions account for approximately 80 percent of the cations found in phloem sap. Using castor bean, Smith and Milburn (1980) found that  $K^+$  and sucrose made up 75 percent of the solute content of phloem sap. The role of K in carbohydrate translocation is not yet fully understood. Ben Zioni et al. (1971) theorized that  $K^+$  is used by the plant as a counter ion for negatively charged organic acids, such as malate, that are being translocated from areas of photosynthesis to the roots to be used in respiration.

Potassium has also been theorized to be involved in phloem loading of carbohydrates (Mengal and Kirkby, 1982). Potassium ions are thought to be transported into phloem sieve cells to counterbalance the negative charge left as  $H^+$  is released by the cells. The transport of  $K^+$  into the sieve cell affects the polarity of the cell membrane allowing increased ATPase activity, carbohydrate protonation and phloem loading to occur. Conti and Geiger (1982) have shown that high concentrations of  $K^+$  at sink sites, increase mobilization of carbohydrates to these regions. High  $K^+$  concentrations have increased synthesis of proteins, fats and cell walls in sink regions (Haeder and Mengal, 1972, Mengal and Haeder, 1977).

There is evidence that type and concentration of ions in media solution affect carbohydrate partitioning. Sorghum grown in several

saline solutions of  $K^+$  and  $Na^+$  salts showed differences in root growth due to ratio and type of salt (Weimberg et al. 1984). Although  $K^+$  and  $Na^+$  both stimulated root growth at high concentrations, only  $K^+$  caused increased root growth at lower concentrations.

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## Chapter II

### Water Relations of Salvia splendens 'Bonfire' as Influenced by Potassium Nutrition and Moisture Stress Conditioning

#### Abstract

The influence of potassium (K) nutrition and moisture stress conditioning (MSC - exposing plants to 4 sublethal dry down cycles) on leaf water relations, transpiration (E), leaf conductance ( $g_1$ ), gravimetric water loss, growth, and nutrient content were determined for the bedding plant salvia (Salvia splendens 'Bonfire'). Increasing K rate and MSC resulted in active osmotic adjustment and consequently increased cellular turgor potentials. Foliar K content increased as osmotic potentials decreased due to treatment indicating that K is an active solute involved in osmotic adjustment for salvia. High K rates and MSC both reduced E,  $g_1$ , and plant gravimetric water loss on a total plant and unit leaf area basis. Greatest shoot dry weight occurred for plants grown with 300 ppm K and no MSC. Total leaf area increased with increasing K rate, but was not affected by MSC.

### Introduction

Plants can tolerate moisture stress and maintain turgor by minimizing transpirational water loss through stomatal changes or by osmotic adjustment (Kramer, 1983). Osmotic adjustment in plants is a decrease in cell osmotic potential (increase in solutes) beyond that explained by the concentrating effect on cell solutes by cellular water loss or reductions in cell volume (Jones and Turner, 1980; Kramer, 1983; Mengel and Kirkby, 1982).

Potassium (K) is very active in plant water relations serving in an osmoregulatory capacity. Potassium's role in stomatal movement has been well documented (Meidner and Willmer, 1975). However, transpirational responses to K nutrition have produced varying results (Bradbury and Malcolm, 1977; Brag, 1972; Koch and Estes, 1975; Rao and Rao, 1983). Increasing K fertilization rates may aid in active osmotic adjustment which maintains positive turgor pressures at low leaf water potentials and improves moisture stress tolerance of some plant species (Lindhauer, 1985; Mengel and Arneke, 1982).

Moisture stress conditioning (MSC - exposing plants to sub-lethal dry-down cycles) has also been reported to promote stomatal and osmotic changes that improve tolerance to moisture stress. Under well watered conditions, reductions in transpirational water losses have been reported for several plant species following MSC (Ackerson and Hebert, 1981; Seiler, 1984; Seiler, 1985). Furthermore, Gupta and Berkowitz (1987) demonstrated that exposing wheat (Triticum aestivum) plants to MSC caused osmotic adjustment and the ability to maintain

essential metabolic processes (including gas exchange) at lower leaf water potentials than in plants not previously exposed to MSC.

Although K nutrition and MSC affect physiological processes directly related to tolerance of moisture stress, results have varied. Furthermore, little work has been published on potential interactions between K nutrition and MSC. The objective of this study was to determine the influence of K nutrition and MSC on water relations, water loss, and growth of salvia (Salvia splendens 'Bonfire').

### Materials and Methods

Seed of salvia were sown on 5 Aug. 1986. Transplanting occurred two weeks later into 500 ml plastic pots containing a 1 peat:1 perlite (v/v) medium amended with 1 kg Micromax (Sierra Chemical Company, Milpitas, CA) and 3 kg dolomitic limestone per m<sup>3</sup>. Pots were placed on benches in a glasshouse and grown under long-day conditions [night interruption from 2200 to 0200 HR using incandescent lights providing approximately 4  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  photosynthetic photon flux (PPF) at the top of the plant canopies] to maintain vegetative growth.

Plants were fertilized with 200 ppm N as  $\text{NH}_4\text{NO}_3$  and 25 ppm P as phosphoric acid in the irrigation water. Potassium rates were 25, 75, 150, 300, 450, and 600 ppm as KCl. Seven weeks after seeding, half of the plants for each K rate were subjected to MSC by exposing plants to four consecutive sub-lethal dry-down cycles. This was accomplished by allowing the plants to reach visible wilt [leaf water potential ( $\psi_1$ ) = -1.1 to -1.4 MPa] before rehydration. Plant water status was monitored during dry-down cycles by determining  $\psi_1$  for three randomly

selected MSC plants twice daily using a pressure chamber (Scholander et al., 1965). No-MSC plants never experienced moisture stress; irrigation occurred as needed with small amounts of tap water to prevent leaching of nutrients from containers. Post-dry-down rehydration was accomplished by submersing MSC and no-MSC plant containers in their respective nutrient solution for approximately 20 minutes.

Treatments were arranged in a randomized complete block design with single-plant replicates for each treatment. There were 12 experimental blocks and 12 treatments (6 K x 2 MSC) for a total of 144 plants.

Components of plant water relations were estimated using modified pressure-volume (PV) techniques as described by Turner (1981) and Tyree and Jarvis (1982). Plants were irrigated and allowed to drain to container capacity at 2030 and 2400 HR on 7 Oct. 1986 to insure that plants were fully hydrated when pre-dawn observations were initiated the following morning. At 0500 HR, plants from four of the twelve experimental blocks were randomly selected and moved to a darkened laboratory. A single recently expanded leaf of similar size was removed from each plant with a razor blade, immediately weighed and then placed in a pressure chamber (Scholander et al., 1965) to determine  $\psi_1$ . Leaf samples were then placed above water in a closed container to retard drying following initial observations. Periodically through the day, each leaf was removed from the container to obtain leaf weight and  $\psi_1$ . Measurements continued for approximately 9 hours until leaves were severely wilted (leaf weights were 70-85 percent of

the initial leaf weight). The leaves were then oven dried and weighed.

PV curves were constructed (Fig. 1) for each leaf by plotting the reciprocal of  $\psi_1$  (ordinate) against the corresponding leaf relative water content (RWC).  $RWC = [(subsequent\ fresh\ weight - dry\ weight) / (initial\ fresh\ weight - dry\ weight)] \cdot 100$ . The equation for the linear portion of each PV curve was determined through regression analysis, while the curvilinear portion of each graph was hand fit. Symplastic water content (SWC) was calculated by subtracting the x-intercept of the line from 100 (RWC at full turgor), while osmotic potential at full turgor ( $\pi_{100}$ ) was determined as the inverse of the y-intercept. Osmotic potential at zero turgor ( $\pi_0$ ) was estimated as the point at which the linear and curvilinear portions of the PV curve join. Leaf turgor potential ( $P_1$ ) for each  $\psi_1$  observation was calculated based on the equation described by Hsiao (1973):  $\psi_1 = \pi + P_1$ .

On 9 Oct. 1986, transpiration (E) and leaf conductance ( $g_1$ ) were obtained with a LI-COR Model 6000 portable photosynthesis system (LI-COR, Inc., Lincoln, NE). Plants were irrigated at 0545 HR and placed under supplemental lighting provided with 100-watt high pressure sodium lamps. Levels of PPF were maintained at  $600\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  or greater. Mean chamber relative humidity and temperature were 45 percent and 30C, respectively. Observations were taken once for each plant in eight of the twelve experimental blocks from 0845 to 1415 HR. Leaf water potentials were determined during each E and  $g_1$  observation with a pressure chamber (Scholander et al., 1965).

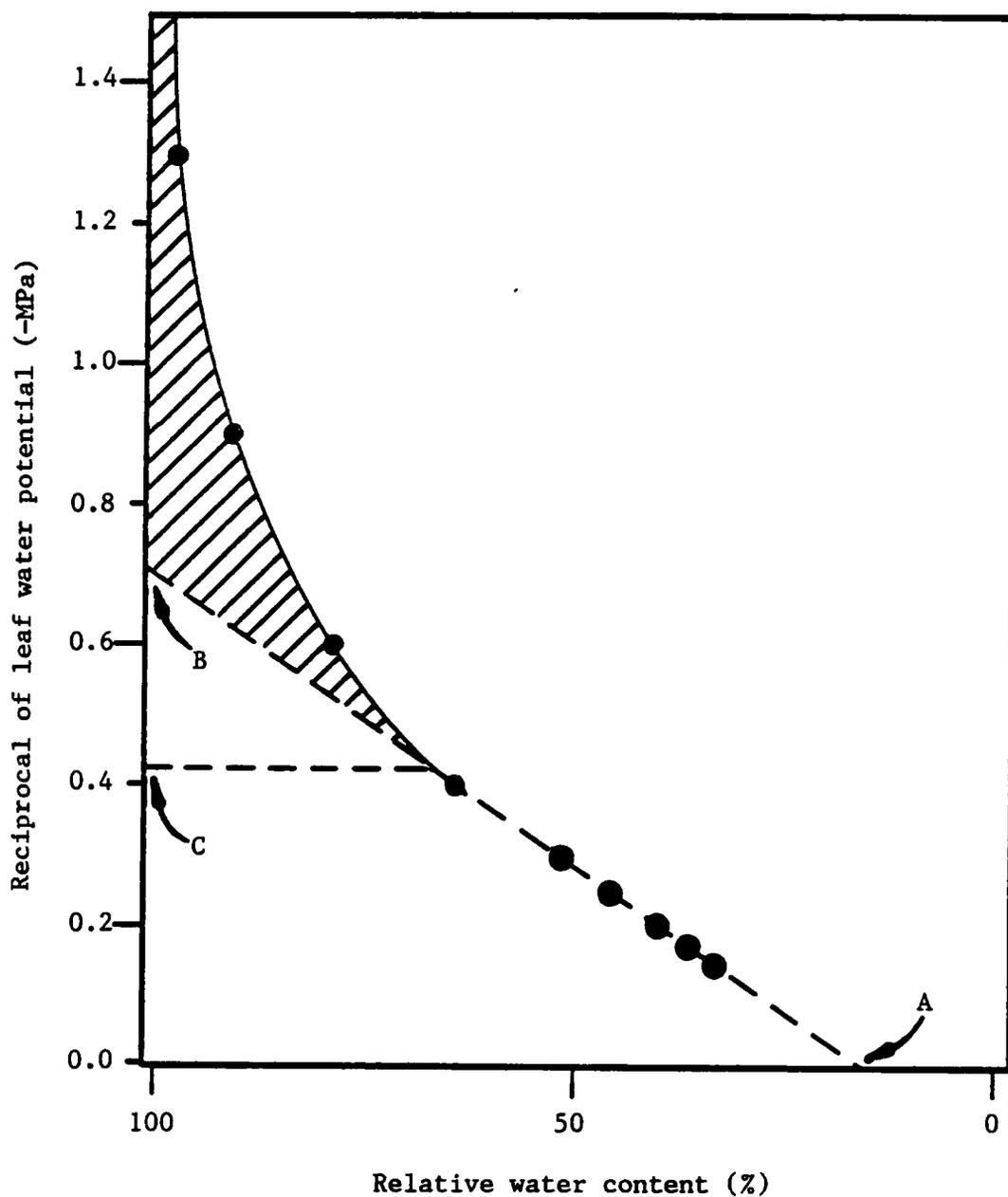


Fig. 1. An example of a pressure-volume curve used for estimation of plant water relations components. Points for estimating symplastic water content, and osmotic potential at full turgor and zero turgor are represented by A, B, and C respectively. The hatched area represents the inverse of the turgor potential. (Redrawn from Turner, 1981.)

Plant gravimetric water loss was determined on the same day that LI-COR observations were made. Pots were allowed to drain to container capacity following irrigation at 0545 HR and initial pot weights taken at 0645 HR. Final pot weights were determined at 1645 HR. Total leaf area was determined for each plant at the termination of the experiment using a LI-COR Model LI-3000 portable leaf area meter. Gravimetric water loss per unit leaf area was then calculated for the ten hour period.

Plants were harvested following final physiological observations to determine shoot dry weight and total leaf area. Foliar K concentrations were determined for plant samples using atomic absorption spectrophotometry.

On 7 Oct. 1986, the day of final rehydration, medium solution samples were collected using the pour-through extraction method (Wright, 1987) to determine medium electrical conductivity (EC) and K concentration. EC (soluble salt levels) were determined using the Agri-Meter (Myron L Co., Carlsbad, CA). Potassium medium concentrations were determined using atomic absorption spectrophotometry.

Data were subjected to analysis of variance (ANOVA) and regression analysis. Homogeneity for regression coefficients of linear regressions was tested by T-test.

### Results

MSC and K had an interactive influence on  $\pi_{100}$  and  $\pi_0$  (Fig. 2). Differences between MSC and no-MSC plants for each of these parameters increased with increasing K rates. SWC was not effected by treatment

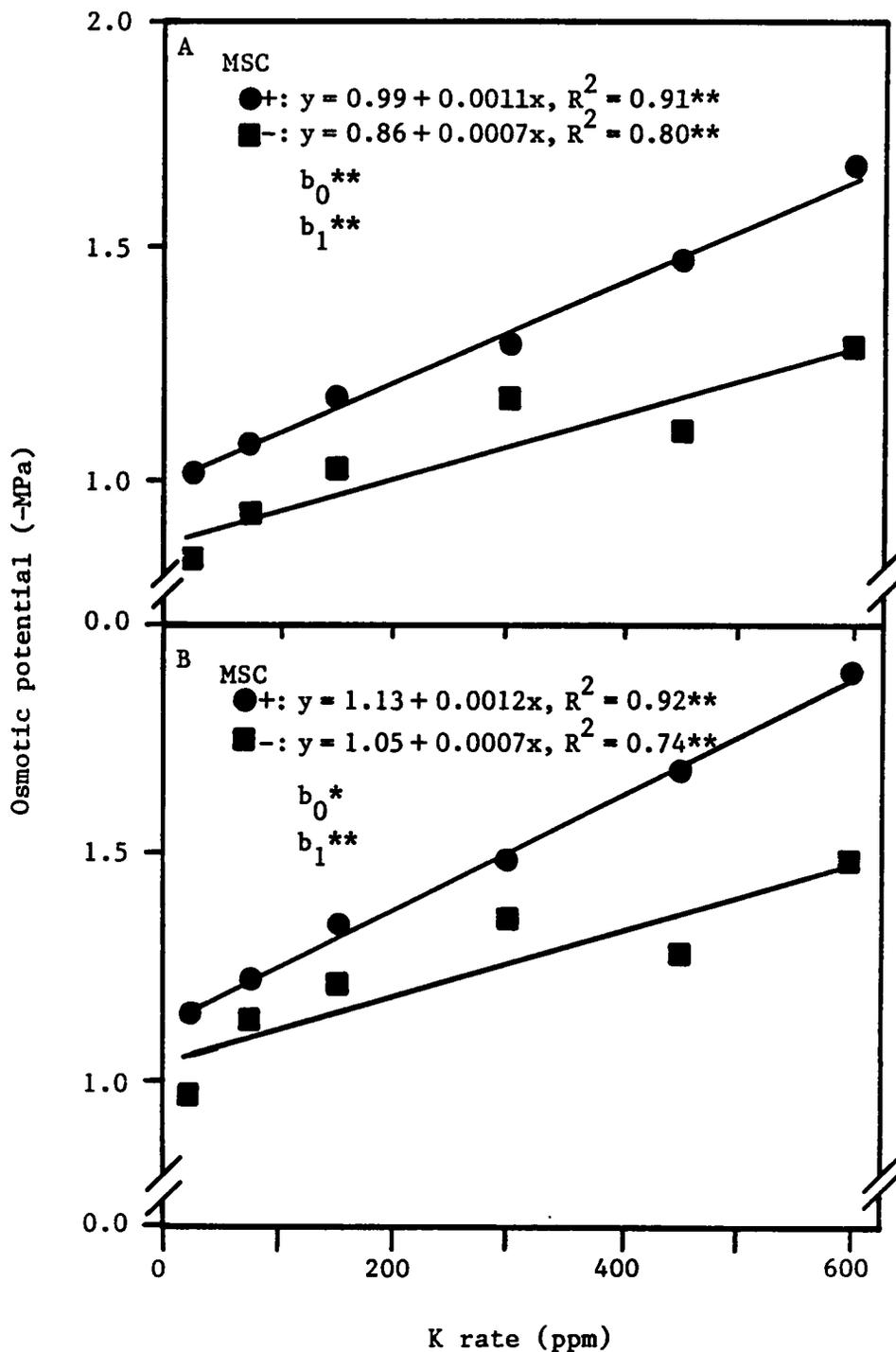


Fig. 2. Leaf osmotic potential at full (A) and zero (B) turgor of *Salvia splendens* 'Bonfire' as influenced by potassium (K) rate and moisture stress conditioning (MSC). Linear regression coefficients (y-intercept =  $b_0$ ; slope =  $b_1$ ) significantly different; 5% (\*) or 1% (\*\*) level.

(data not shown). While  $P_1$  and  $\psi_1$  were always well correlated, the relationship was heightened at any given  $\psi_1$  as K rate increased or MSC was imposed (Fig. 3; Table. 1). Differences in the  $P_1$  to  $\psi_1$  relationship for MSC plants compared to no-MS C plants increased as K rate increased.

No interactions between K and MSC were observed for E,  $g_1$ , or plant gravimetric water loss. E, and  $g_1$  responded quadratically to increasing K rates with observed maximum values for each occurring at 150 and 300 ppm, respectively (Table 2). Gravimetric water loss per unit leaf area decreased linearly as K rate increased, while observed gravimetric water loss for the total plant increased in response to K rates up to 150 ppm, but not beyond. MSC plants had lower E and  $g_1$  than no-MS C plants. Reduced E for MSC compared to no-MS C plants was supported by a 30 percent reduction in gravimetric water loss per unit leaf area and a 32 percent reduction in gravimetric water loss on a total plant basis.

Shoot dry weight and total leaf area were significantly affected by K and MSC in the absence of an interaction (Table 2). Maximum observed dry weight yield occurred at 300 ppm K, while MSC inhibited dry weight accumulation by approximately 27 percent compared to no-MS C plants when averaged over the 6 K rates. Total leaf area per plant increased linearly with increasing K rates. MSC had no effect on leaf area.

MSC by K interactions occurred for medium EC, medium K concentration, and foliar K concentration (Table 3). Each of these three parameters increased linearly with increasing K rate for both MSC and no-

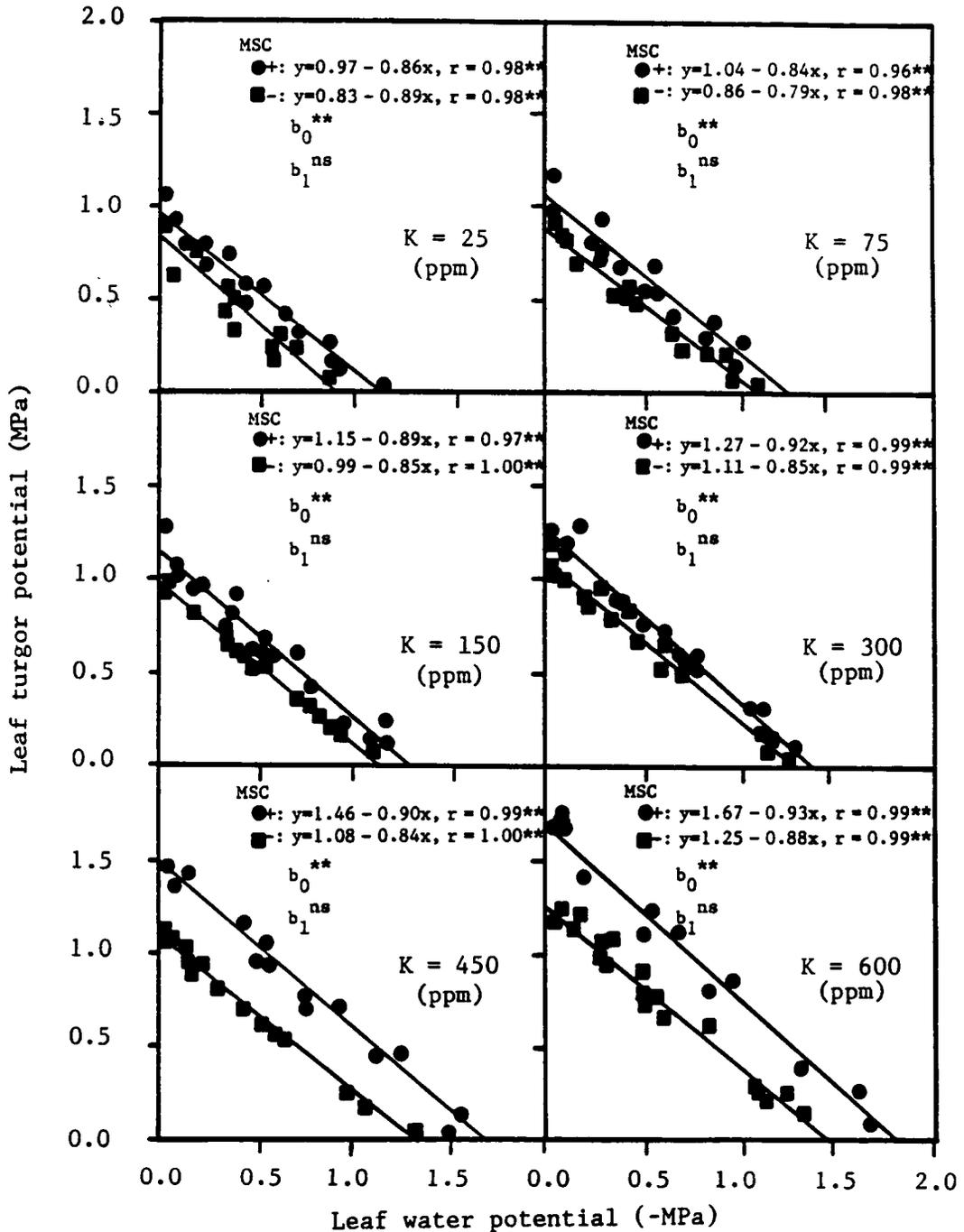


Fig. 3. The relationship between leaf turgor potential and water potential of *Salvia splendens* 'Bonfire' as influenced by potassium (K) rate and moisture stress conditioning (MSC). Linear regression fit significant at the 1% (\*\*). Regression coefficients (y-intercept =  $b_0$ ; slope =  $b_1$ ) nonsignificant (ns), or significant at the 1% (\*\*). level.

Table 1. Comparison of linear regression coefficients (y-intercept =  $b_0$ ; slope =  $b_1$ ) for the relationship between leaf turgor pressure and water potential of Salvia splendens 'Bonfire' as influenced by potassium (K) rate and moisture stress conditioning (MSC).

MSC	K rate (ppm)	Reg. Coeff.	K rate (ppm)					
			75	150	300	450	600	
+MSC	25	$b_0$	NS <sup>z</sup>	**	**	**	**	
		$b_1$	NS	NS	NS	NS	NS	
	75	$b_0$	-	**	**	**	**	
		$b_1$	-	NS	NS	NS	NS	
	150	$b_0$	-	-	**	**	*	
		$b_1$	-	-	NS	NS	NS	
	300	$b_0$	-	-	-	**	NS	
		$b_1$	-	-	-	NS	*	
	450	$b_0$	-	-	-	-	**	
		$b_1$	-	-	-	-	*	
	-MSC	25	$b_0$	NS	**	**	**	**
			$b_1$	NS	NS	NS	NS	NS
75		$b_0$	-	**	**	**	**	
		$b_1$	-	NS	NS	NS	NS	
150		$b_0$	-	-	**	**	**	
		$b_1$	-	-	NS	NS	NS	
300		$b_0$	-	-	-	NS	**	
		$b_1$	-	-	-	NS	NS	
450		$b_0$	-	-	-	-	**	
		$b_1$	-	-	-	-	NS	

<sup>z</sup>NS, \*, and \*\* represent nonsignificance and significance at the 5% and 1% level by T-test, respectively.

Table 2. Transpiration, daily gravimetric water loss on a total plant and unit leaf area basis, leaf conductance, shoot dry weight, and total leaf area of *Salvia splendens* 'Bonfire' as influenced by potassium (K) rate and moisture stress conditioning (MSC).

Treatment	Transpiration ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	Daily gravimetric water loss <sup>z</sup>			Leaf conductance ( $\text{cm}\cdot\text{s}^{-1}$ )	Shoot dry wt. (g)	Total leaf area ( $\text{cm}^2$ )
		Total plant (g)	Leaf area ( $\text{mg}\cdot\text{cm}^{-2}$ )	Leaf area			
K rate (ppm)							
25	8.7	77	120	0.93	4.5	650	
75	10.5	89	119	1.25	5.1	740	
150	10.9	103	128	1.50	5.3	810	
300	11.1	101	112	1.45	5.4	900	
450	10.4	100	109	1.29	5.2	920	
600	8.3	99	101	0.89	5.2	1030	
MSC							
+	9.3	77	95	1.05	4.3	820	
-	10.7	113	135	1.39	5.9	860	
Significance							
K rate		Q*	L*	Q**	Q*	L**	
Regression <sup>y</sup>	Q**						
R <sup>2</sup>	0.15	0.13	0.08	0.18	0.12	0.45	
MSC <sup>x</sup>	**	**	**	**	**	NS	

<sup>z</sup>Means determined over a 10 hour period (0800-1800 HR).

<sup>y</sup>L and Q represent significant linear and quadratic regression fits, respectively, at the 5% (\*) or 1% (\*\*) level.

<sup>x</sup>NS and \*\* represent nonsignificance and significance at the 1% level by F-test.

Table 3. Medium electrical conductivity (EC), medium potassium (K) concentration, and foliar K concentration of Salvia splendens 'Bonfire' as influenced by K rate and moisture stress conditioning (MSC).

Treatment	Medium EC ( $\text{dS}\cdot\text{m}^{-1}$ )		Medium [K] (ppm)		Foliar [K] (%)	
	+MSC	-MSC	+MSC	-MSC	+MSC	-MSC
K rate (ppm)						
25	1.20 <sup>z</sup>	0.95	17	16	1.28	0.93
75	1.23	1.18	48	36	2.18	1.28
150	1.88	1.25	134	82	3.55	2.08
300	2.73	1.65	367	158	4.75	4.10
450	3.70	2.45	633	415	5.53	4.88
600	4.65	3.05	852	672	6.10	5.50
Significance						
Regression <sup>y</sup>	L**	L**	L**	L**	L**	L**
R <sup>2</sup>	0.96	0.88	0.95	0.92	0.91	0.94

<sup>z</sup>Simple effects of MSC for each rate of K are significantly different at the 1% level by F-test.

<sup>y</sup>L\*\* represents significant linear regression fit at the 1% level.

MSC plants. MSC plants had greater medium EC, medium K concentration, and foliar K concentration compared to no-MSC plants.

### Discussion

Salvia osmotically adjusted as a result of increasing K rate and MSC based on reductions in  $\pi_{100}$  and  $\pi_0$  with no change in SWC (osmotically active water) (Hsiao, 1973; Weatherley, 1970). Although increasing K rates (Lindhauer, 1985; Mengel and Arneke, 1982) and moisture stress (Ackerson and Hebert, 1981; Turner et al., 1987; Jones and Turner, 1980; Seiler, 1985) have been separately reported to cause osmotic adjustment in some plants, our results show a synergistic effect between increasing K and MSC.

Osmotic changes for salvia in response to increasing K rate and MSC resulted in plants that were able to maintain positive  $P_1$  to lower  $\psi_1$  than plants grown with low K rates and no-MSC, which should increase tolerance to moisture stress. In fact, before plants were harvested, and following physiological data collection, plants grown with increasing K rate and MSC wilted later than plants grown with low K and no-MSC as moisture deficits developed (data not shown). Maintenance of  $P_1$ -dependent physiological processes, including gas exchange, at low  $\psi_1$  due to osmotic adjustment have been shown with increasing K rate (Lindhauer, 1985) as well as following MSC (Ackerson and Hebert, 1981; Gupta and Berkowitz, 1987; Seiler 1984; Seiler, 1985; Turner et al., 1978).

The influence of increasing K rate and MSC on plant  $\pi$  and consequently  $P_1$  was probably due to high medium solution EC and K con-

centrations for plants receiving increasing K rate and MSC. Potassium ions have been reported as one solute involved in osmotic adjustment for several plant species subjected to osmotic stress (Bernstein, 1963; Kaiser, 1982; Sangita et al., 1983; Weimberg et al., 1982). Increased medium EC or soluble salts, including K, would increase solute accumulation by the plant, lowering the water potential of the roots, stimulating water uptake and increasing  $P_1$  (Campbell et al., 1949; Mengel and Kirkby, 1982). The increasing foliar K concentrations as a result of increasing K rate and MSC suggest that K is an important solute involved in osmotic adjustment for salvia.

Reductions in  $E$ , and gravimetric water loss on a total plant and unit leaf area basis, following MSC, were supported by reduced  $g_1$ . The main factor controlling  $g_1$  is stomatal aperture and changes in  $g_1$  have been well correlated to changes in stomatal aperture (Kramer, 1983; Larcher, 1983). Stomatal movement is controlled by a number of complicated interactions between the plant and the environment; however, plant water status is the fundamental factor ultimately controlling stomatal movement. Water deficits generally supersede all other factors affecting stomatal movement (Larcher, 1983).

Water deficits are apparently not responsible for treatment differences observed for  $E$  and  $g_1$  in this study. Mean  $\psi_1$  for the final experimental block of plants used for  $E$  and  $g_1$  measurements was -0.67 MPa, while the onset of stomatal closure for herbaceous dicots has reportedly occurred at  $\psi_1$  from -0.7 to -1.6 MPa (Hsiao, 1973). Seiler (1984) observed similar reductions in  $g_1$  for loblolly pine under well watered conditions following MSC, and suggested that these

reductions may be due to osmotic changes in the leaves. He hypothesized that osmotic adjustment in mesophyllic and/or epidermal cells surrounding the cells of the stomatal apparatus (guard and subsidiary cells) may reduce turgor potential gradients required between these cell groups for stomatal opening to occur. In our study, osmotic adjustment was also observed for MSC plants and may explain reductions in  $g_1$  observations for salvia following MSC.

In this study,  $g_1$  reductions following MSC may also be attributed to accumulation of abscissic acid (ABA) during dry-down cycles, a phenomenon known to cause stomatal closure (Meidner and Willmer, 1975). Consequently, residual ABA following MSC may temporarily prevent full recovery of stomatal function (Johnson and Ferrell, 1982). However, since ABA was not examined in this experiment, the changes in  $g_1$  cannot be explained by either.

Total leaf area increased linearly with increasing K rates. However, gravimetric water loss per unit area of leaf declined with increasing K rate and gravimetric water loss on a whole plant basis did not increase beyond 150 ppm K. Reasons for reductions in gravimetric water loss with high K rates despite increasing leaf area could include: greater osmotic adjustment reducing stomatal apertures as previously discussed for MSC plants, leaf size or arrangement causing differences in boundary layer resistance to transpirational water loss or mutual shading, and/or higher K concentrations in the tissue causing stomata to be more sensitive to environmental conditions (Bradbury and Malcolm, 1977).

The magnitude of gravimetric water loss per unit leaf area was not comparable to the LI-COR  $E$  estimates. However, as previously mentioned,  $E$  observations were made when plants were not under moisture stress and measurements were made on a single leaf. Gravimetric water loss encompassed a ten-hour period during the day, the latter part of which moisture stress may have occurred or environmental conditions changed. Furthermore, a portion of these differences could be accounted for by environmental differences between the greenhouse and LI-COR cuvette used for determining  $E$ .

In conclusion, increasing  $K$  rates, MSC, or a combination of the two may improve tolerance to moisture stress of the bedding plant salvia through physiological acclimations. Although plants in this study were not exposed to moisture stress following treatment, reductions in water loss and the ability to osmotically adjust should allow salvia to maintain turgor during the onset of moisture stress and continue essential metabolic processes. More research is needed to determine how these physiological adaptations will actually effect salvia when exposed to moisture stress.

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## Chapter III

### Moisture Stress Conditioning and Tolerance of Salvia splendens 'Bonfire' to Moisture Stress

#### Abstract

The objective of this study was to determine the influence of moisture stress conditioning (MSC - exposing plants to 4 sub-lethal dry-down cycles) on gas exchange, hourly gravimetric water loss, and growth of the bedding plant Salvia splendens 'Bonfire' during moisture stress. On day one following final irrigation, no differences in leaf water potentials ( $\psi_1$ ) were observed due to MSC. However, MSC plants had lower mid-day net photosynthesis (Pn), transpiration (E), leaf conductance ( $g_1$ ), and hourly gravimetric water loss per unit leaf area than controls. Percentage of stomatal inhibition of photosynthesis (SI) for MSC plants was greater than for control plants along with the lack of differences in mesophyllic resistance to CO<sub>2</sub> ( $r_m$ ) due to treatment indicate gas exchange differences on day one were stomatal in nature. MSC plants exhibited greater Pn, E,  $g_1$ , and hourly gravimetric water loss per unit leaf area, while SI and  $r_m$  were lower than controls throughout day two. MSC plants maintained positive Pn rates and turgor to lower  $\psi_1$  than control plants on day two. Greater water use efficiency estimates were observed for MSC plants compared to controls throughout the two day study.

### Introduction

Wholesale growers are becoming more aware of the need for improved post-production performance of bedding plants (Armitage, 1986; Hammer, 1988). Moisture stress is a major factor in quality loss following wholesale production (Nelson and Carlson, 1987). Current recommendations for improving post-production performance include reducing irrigation frequency, fertilization, and greenhouse temperatures during the final few weeks of production (Armitage, 1987; Seeley, 1985). Such "hardening off" steps prepare plants for suboptimal conditions often encountered during shipping, in the retail market place, and/or during landscape establishment.

These recommendations are in part based on the response of Petunia X hybrida seedlings grown under low frequency irrigation regimes (Armitage and Kowalski, 1983). Visual quality was maintained longer and dry matter production was greater for plants grown with a low irrigation frequency regime compared to a high frequency regime during a 15-day period following wholesale production. However, plants grown under the low irrigation regime were small at the end of the production cycle and were not exposed to moisture stress following production.

Although moisture stress conditioning (MSC) is currently recommended to growers, little is known about the influence of MSC on essential physiological processes required to facilitate the maintenance of post-production bedding plant quality. MSC improved physiological processes directly related to moisture stress tolerance of agronomic crops (Ackerson and Hebert, 1981; Brown et al., 1976; Gupta

and Berkowitz, 1987; Matthews and Boyer, 1984) and woody species (Osonubi and Davies, 1981; Seiler, 1985; Seiler and Johnson, 1988). The objective of this study was to determine the influence of MSC on gas exchange, hourly gravimetric water loss, and growth of salvia (Salvia splendens 'Bonfire') during moisture stress.

### Materials and Methods

Seed of salvia were sown on 11 Jan. 1988 and glasshouse grown as described by Eakes et al. (1989). Plants were fertilized with 200 ppm N as  $\text{NH}_4\text{NO}_3$ , 25 ppm P as phosphoric acid, and 150 ppm K as KCl in the irrigation water. Seven weeks after seeding half of the 40 plants were subjected to MSC as described Eakes et al. (1989). Treatments were arranged in a randomized complete block design with 20 single-plant replicates for each treatment.

Plants were irrigated at 0545 HR and placed under supplemental lighting provided with 1000-watt high pressure sodium lamps. Levels of photosynthetic photon flux (PPF) were maintained at  $600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  or greater. Net photosynthesis (Pn), transpiration (E), leaf conductance ( $g_1$ ), chamber  $\text{CO}_2$  concentration (CA), and internal  $\text{CO}_2$  (CI) were obtained with a LI-COR Model 6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE). Mean chamber relative humidity, temperature, and  $\text{CO}_2$  concentrations were 36 percent, 26 C, and 361 ppm, respectively. Water use efficiency (WUE) estimates were calculated by dividing simultaneous LI-COR Pn observations by E rates. Mesophyllic resistance to  $\text{CO}_2$  ( $r_m$ ) and stomatal inhibition of Pn (SI) were determined as follows:  $r_m = \text{CI}/\text{Pn}$  (Osonubi and Davies, 1980),

and  $SI = [(CA - CI) / CA] \cdot 100$  (Jones, 1985). Gas exchange observations were taken hourly for each plant in 10 of the experimental blocks from 0900 to 1600 HR on 21 Mar. and from 0900 to 1200 HR on 22 Mar. 1988. To prevent significant losses in total leaf area during  $\psi_1$  observations with the pressure chamber (Scholander et al., 1965), three plants per treatment were randomly selected for readings at 0630, 1200, and 1630 HR on both days of the experiment.

Plant gravimetric water loss was determined for the remaining 10 experimental blocks on the same days that LI-COR observations were made. Pots were allowed to drain to container capacity following irrigation at 0545 HR and initial pots weights taken at 0645 HR. Subsequent pot weights were made hourly from 0800 to 1700 HR on 21 Mar. and from 0800 to 1200 HR on 22 Mar. 1988. Total leaf area was determined for each plant at the termination of the experiment using a LI-COR Model LI-3000 portable leaf area meter. Hourly gravimetric water loss per unit leaf area was then calculated.

Total leaf area and total shoot dry weight were determined for plants of all 20 experimental blocks following final physiological observations.

Data were subjected to analysis of variance (ANOVA). Gas exchange and water status data were analyzed within each observation time.

### Results

E (Fig. 1) and  $g_1$  (Fig. 2) during day one following final irrigation were lower for MSC plants than control plants except at 1600 HR.

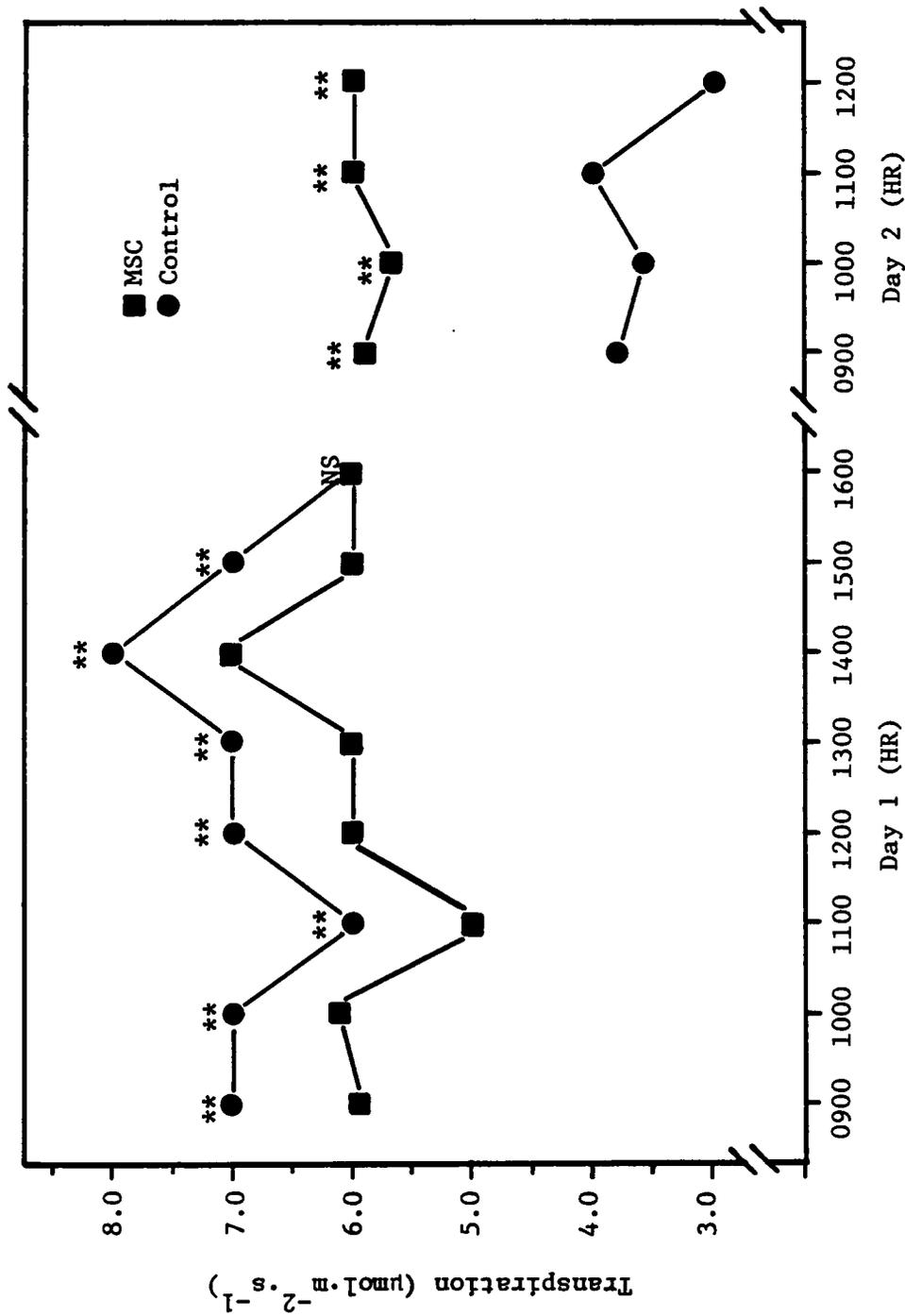


Fig. 1. Transpiration of *Salvia splendens* 'Bonfire' as influenced by moisture stress conditioning (MSC) during the onset of moisture stress. Differences between treatment means within an observation time nonsignificant (NS), or significant at the 5% (\*) or 1% (\*\*) level as determined by F-test.

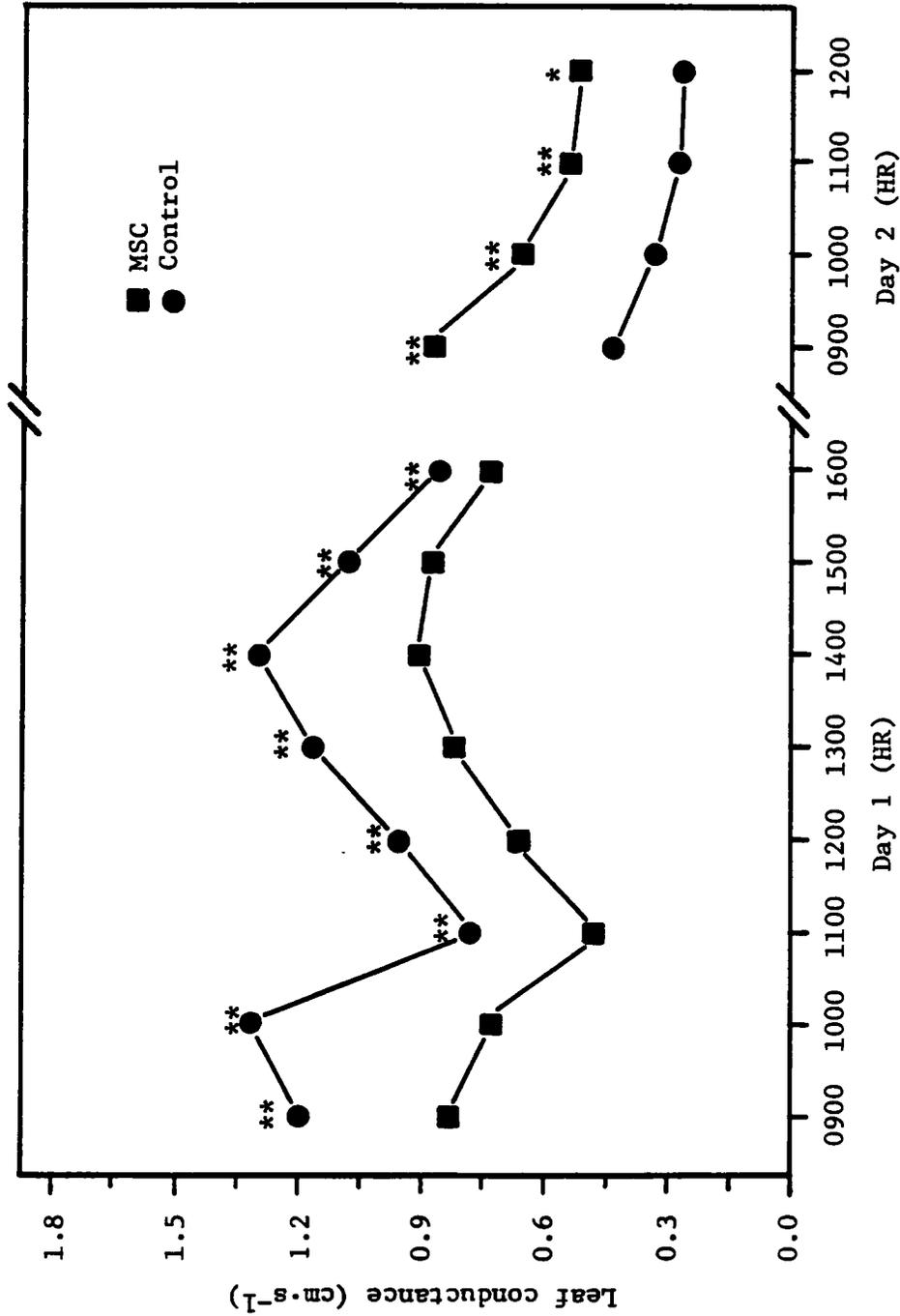


Fig. 2. Leaf conductance of *Salvia splendens* 'Bonfire' as influenced by moisture stress conditioning during the onset of moisture stress. Differences between treatment means within an observation time nonsignificant (NS), or significant at the 5% (\*) or 1% (\*\*) level as determined by F-test.

Initial E rates for MSC plants on day two were similar to those reported at the end of day one, but initial E for control plants on day two were 54 percent lower than the previous day. Leaf conductance for MSC plants on day two was also greater than for controls and declined over time for both treatments.

Hourly gravimetric water losses for MSC plants were less than for control plants primarily up to 1300 HR on day one, but were greater throughout day two (Fig. 3). By the end of day one, MSC plants had lost an average of 69 fewer grams of water (38 percent) than control plants on a whole plant basis (data not shown).

Mid-day Pn was lower for MSC plants than controls on day 1 (Fig. 4) but, as with E, were much greater throughout day two. All MSC plants maintained positive Pn rates throughout day two with a final mean rate of  $2.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at 1630 HR (data not shown). SI was greater for MSC plants compared to controls throughout day one, but there were no differences in  $r_m$  due to MSC (Table 1). On day two,  $r_m$  was lower, while SI remained greater for MSC plants compared to controls. WUE was greater for MSC plants than controls throughout most of day one and all of day two, with dramatic differences on day two (Fig. 5).

MSC had no affect on  $\psi_1$  during day one (Table 2). However, on day two  $\psi_1$  for control plants was lower than those for MSC plants during the first observation of the day taken at 0630 HR. Although this was the extent of  $\psi_1$  effects, control plants were visibly wilted at 1200 HR with a mean  $\psi_1$  of -1.28 MPa; MSC plants showed no visible tur-

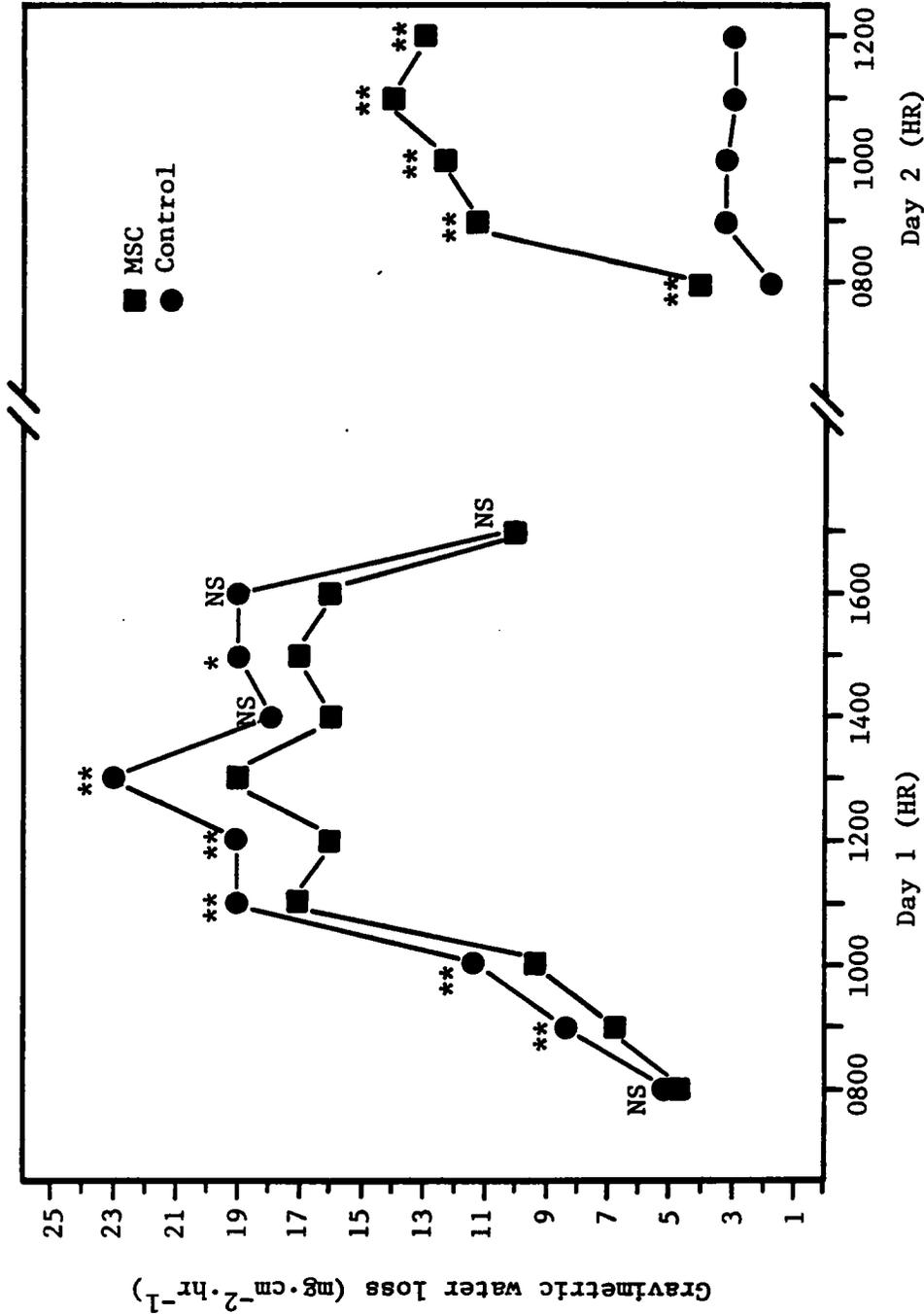


Fig. 3. Hourly gravimetric water loss for *Salvia splendens* 'Bonfire' as influenced by moisture stress conditioning (MSC) during the onset of moisture stress. Differences between treatment means within an observation time non-significant (NS), or significant at the 5% (\*) or 1% (\*\*) level as determined by F-test.

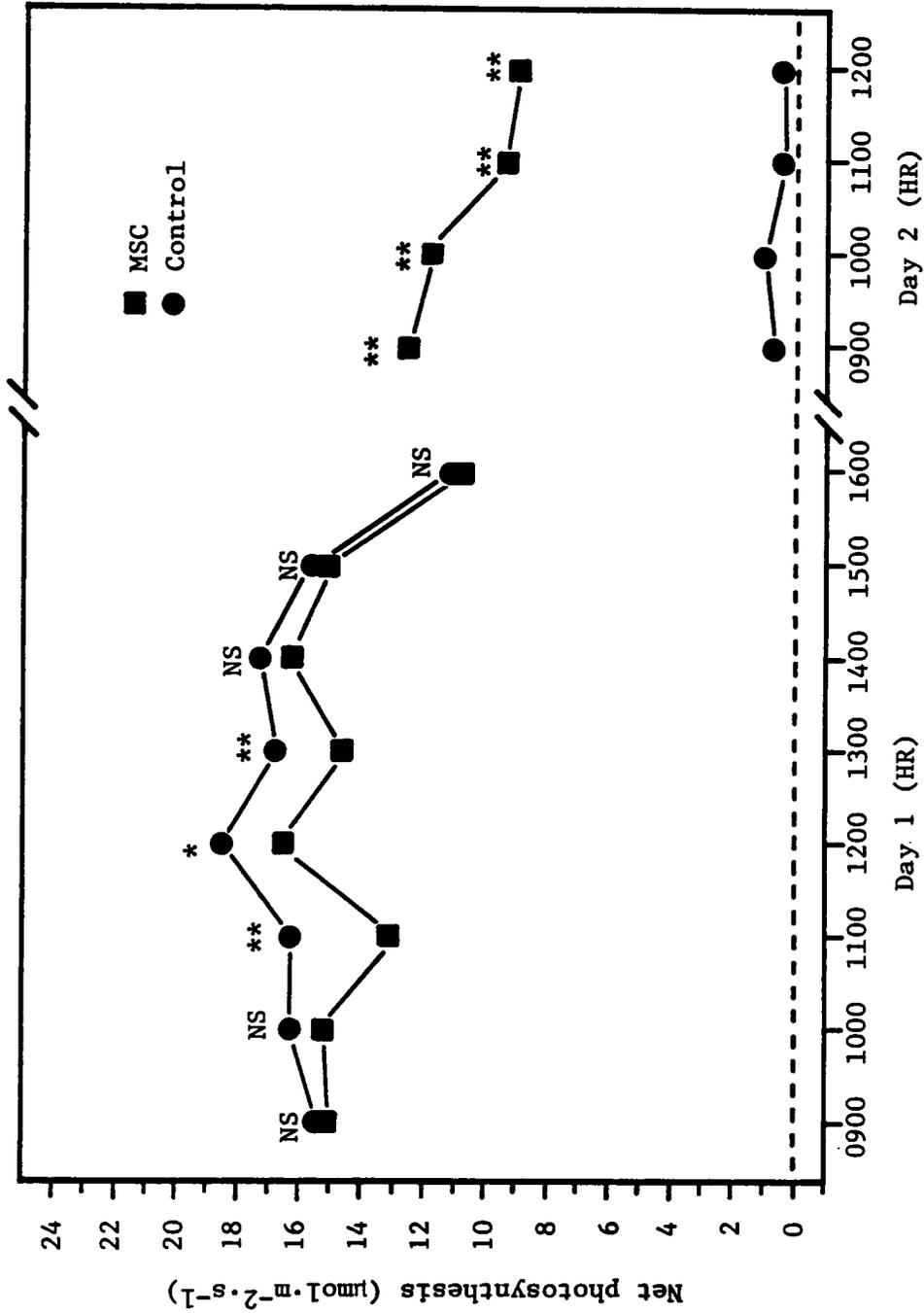


Fig. 4. Net photosynthesis of *Salvia splendens* 'Bonfire' as influenced by moisture stress conditioning (MSC) during the onset of moisture stress. Differences between treatment means within an observation time nonsignificant (NS), or significant at the 5% (\*) or 1% (\*\*) level as determined by F-test.

Table 1. Mesophylllic resistance to CO<sub>2</sub> and stomatal inhibition of photosynthesis of Salvia splendens 'Bonfire' as influenced by moisture stress conditioning (MSC) during the onset of moisture stress.

Treatment	Mesophylllic resistance to CO <sub>2</sub> (s·cm <sup>-1</sup> )											
	Day 1 (HR)					Day 2 (HR)						
	0900	1000	1100	1200	1300	1400	1500	1600	0900	1000	1100	1200
MSC	7.1	7.2	7.6	6.1	7.6	6.7	7.9	11.1	9.7	9.7	12.2	14.6
Control	7.5	7.1	6.6	5.9	6.9	6.6	7.9	10.7	162.9	94.5	118.6	120.4
Significance	NS <sup>z</sup>	NS	NS	NS	NS	NS	NS	NS	**	**	**	**

Treatment	Stomatal inhibition photosynthesis (%)											
	Day 1 (HR)					Day 2 (HR)						
	0900	1000	1100	1200	1300	1400	1500	1600	0900	1000	1100	1200
MSC	27	30	36	34	27	25	24	21	21	25	25	25
Control	20	26	30	28	23	22	21	20	5	8	7	7
Significance	**	**	**	**	**	**	**	*	**	**	**	**

<sup>z</sup>NS, \*\* and \* represent nonsignificance and significance at the 5% and 1% levels by F-test, respectively.

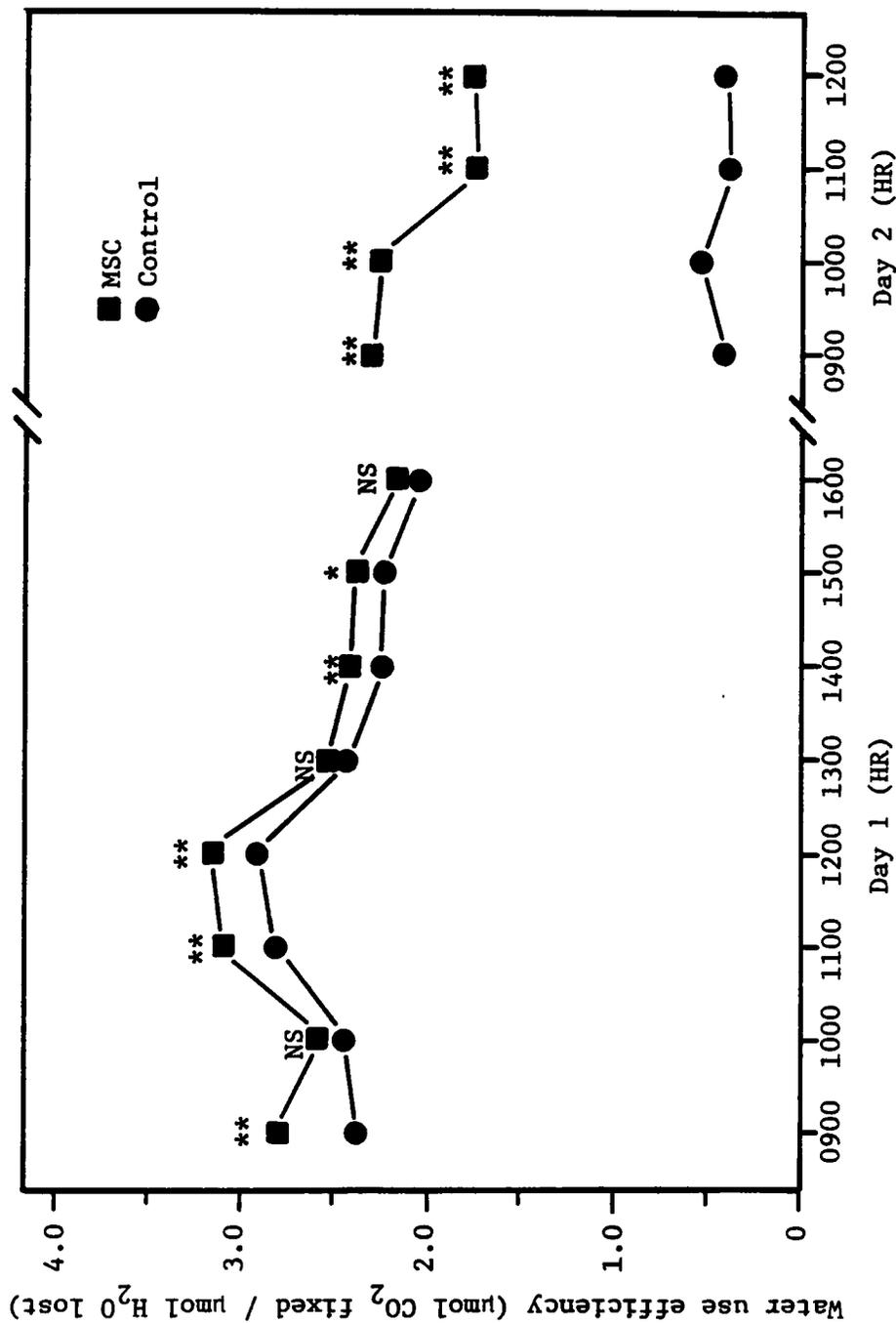


Fig. 5. Water use efficiency of *Salvia splendens* 'Bonfire' as influenced by moisture stress conditioning (MSC) during the onset of moisture stress. Differences between treatment means within an observation time nonsignificant (NS), or significant at the 5% (\*) or 1% (\*\*) level as determined by F-test.

Table 2. Leaf water potential of Salvia splendens 'Bonfire' as influenced by moisture stress conditioning (MSC) during the onset of moisture stress.

Treatment	Leaf water potential (-MPa)					
	Day 1 (HR)			Day 2 (HR)		
	0630	1200	1630	0630	1200	1630
MSC	0.14 <sup>z</sup>	1.06	0.62	0.22	0.98	1.30
Control	0.22	0.77	0.59	0.64	1.28 <sup>y</sup>	-
Significance	NS <sup>x</sup>	NS	NS	*	NS	-

<sup>z</sup>Means at each time are for 3 randomly selected plants per treatment.

<sup>y</sup>All control plants showing visible wilt.

<sup>x</sup>NS and \* represent nonsignificance and significance at the 5% level by F-test, respectively.

gor loss at  $\psi_1 = -0.98$  MPa. MSC plants were still turgid at the end of the experiment (2130 HR) with a mean  $\psi_1$  of  $-1.30$  MPa.

MSC reduced shoot dry weight and total leaf area by 42 and 25 percent, respectively compared to controls (Table. 3).

### Discussion

MSC should improve tolerance of salvia to moisture stress through reductions in water loss as indicated by lower E and hourly gravimetric water loss during day one compared to control plants. These reductions in E appear to be due to lower  $g_1$  for MSC plants compared to controls, a hypothesis supported by similar responses observed for salvia in a previous study (Eakes et al., 1989) and for two tree species (Seiler, 1985; Seiler and Johnson, 1988). Low  $g_1$  rates as seen in this experiment have been well correlated with reduced stomatal apertures (Burrows and Milthorpe, 1976) which could account for reduced water loss by MSC plants.

Reductions in stomatal aperture during day one could also explain reductions in mid-day Pn for MSC plants compared to controls. Stomatal rather than nonstomatal inhibition of Pn for MSC plants is substantiated by increased SI compared to controls, with no differences in  $r_m$  due to treatment. Although Pn during mid-day for MSC plants was lower than for controls, WUE was greater. This indicates that E was reduced to a greater extent than Pn by MSC.

Results were dramatically different on day two. Reductions in water loss for MSC plants during day one allowed maintenance of higher  $\psi_1$  than for control plants as early as 0630 HR on day two, facilitat-

Table 3. Shoot dry weight and total leaf area of Salvia splendens 'Bonfire' as influenced by moisture stress conditioning (MSC).

Treatment	Shoot dry wt. (g)	Total leaf area (cm <sup>2</sup> )
MSC	4.7	941
Control	8.1	1267
Significance	**Z	**

Z\*\* represents significance at the 1% level by F-test.

ing continued E and Pn. Reductions in E, Pn, and  $\psi_1$  on day two may be, in part, due to plant size (large control plants expending available water first). But, physiological measurements such as E and hourly gravimetric water loss during day one were based on unit leaf area and were recorded before control plants exhibited water deficits. Therefore, reduced water loss by MSC plants during day one had to be, in part, due to treatment and not just plant size.

Initial E and  $g_1$  observations for MSC plants on day two were similar to those recorded on day one, while being drastically reduced for control plants. Reductions in mean  $\psi_1$  at 0630 HR on day two for control plants suggests that control plants were unable to fully rehydrate overnight inhibiting stomatal opening on day two. The onset of stomatal closure for annual plants has been reported to occur at  $\psi_1$  of -0.7 to -1.6 MPa (Hsiao, 1973). The hypothesis that water was sufficiently limiting for control plants to prevent stomatal opening, is supported by reductions in E,  $g_1$ , and hourly gravimetric water loss on day two. Although Pn for control plants was also lower on day two, nonstomatal limitations to Pn appear to be greater than stomatal limitations. Mesophyllic resistance to  $\text{CO}_2$  was more than ten times greater and SI dropped by 70 to 75 percent on day two compared to day one indicating direct disruption of the photosynthetic mechanism rather than reductions of internal  $\text{CO}_2$  concentrations during stomatal closure limiting Pn.

Maintenance of greater Pn rates for MSC plants during day two was not due only to reductions in water loss during day one, but also to the ability of plants to maintain Pn at low  $\psi_1$ . By 1630 HR on day

two, MSC plants maintained a mean Pn rate of  $2.5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  with a mean  $\psi_1$  of -1.30 MPa. By contrast, at 1200 HR on day two, control plants had a mean  $\psi_1$  of -1.28 MPa and a mean Pn of  $0.4 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ . This photosynthetic acclimation to low  $\psi_1$  for MSC plants appears to be due to both stomatal and nonstomatal changes with lower  $r_m$  and greater  $g_1$  for MSC plants at similar  $\psi_1$  compared to those for control plants. Photosynthetic acclimation to low  $\psi_1$  following MSC has also been reported for several agronomic crops (Ackerson and Hebert, 1981; Ashton, 1956; Brown et al., 1976; Gupta and Berkowitz, 1987; Matthews and Boyer, 1984) and woody plant species (Seiler and Johnson, 1988). Despite the lack of agreement attributing these Pn adaptations to stomatal or nonstomatal factors, the consensus of these authors agree that osmotic adjustment is involved by allowing the plant to maintain turgor during moisture deficits (Brown et al., 1976; Gupta and Berkowitz, 1987; Matthews and Boyer, 1984). Based on previous work demonstrating that salvia osmotically adjusts and maintains turgor during low  $\psi_1$  following MSC (Eakes et al., 1989), photosynthetic acclimation in this experiment could also have been due to osmotic adjustment in response to MSC.

On day two, maintenance of higher  $g_1$  and Pn rates for MSC plants resulted in greater WUE estimates than those for control plants. Several other authors have also reported increased WUE following MSC (Clemens and Jones, 1978, Seiler and Johnson, 1988).

Plant dry weight was reduced by MSC, a fact which is quite common (Eakes et al., 1989; Osonubi and Davies, 1978; Seiler, 1985; Seiler and Johnson, 1988), but not universal (Clemens and Jones, 1978; Oso-

nubi and Davies, 1978). Reduction in plant growth during MSC is probably due to loss of turgor during subsequent dry-down cycles. Turgor loss during moisture stress has been shown to reduce cell division and elongation, as well as essential metabolic processes required for plant growth and development (Hsiao, 1973).

Although, MSC reduced plant size for salvia, use of MSC could prove important to wholesale growers. In this experiment, MSC of salvia improved moisture stress tolerance through dehydration avoidance as well as dehydration tolerance allowing essential metabolic processes to continue longer than control plants. Improvements in moisture stress tolerance should allow visual quality to be maintained longer and reduce plant mortality following wholesale production.

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## Chapter IV

### Potassium Nutrition and Tolerance of Salvia splendens 'Bonfire' To Moisture Stress

#### Abstract

The objective of this study was to determine the influence of potassium (K) rate on gas exchange, hourly gravimetric water loss, and growth of Salvia splendens 'Bonfire' during moisture stress. On day one following final irrigation, plants grown with K rates of 300 and 600 ppm had lower transpiration (E), hourly gravimetric water loss, leaf conductance ( $g_1$ ), and net photosynthesis (Pn) compared to plants grown with 75 ppm K. Reductions in gas exchange parameters and hourly gravimetric water loss with the high K rates appear to be due to stomatal adaptations based on lower  $g_1$ . On day two, plants grown with 600 ppm K had greater Pn, E, and  $g_1$  as the experiment was terminated compared to plants receiving 75 ppm K, although leaf water potential was similar. Potassium rate had little affect on water use efficiency. Shoot dry weight and total leaf area were greatest for plants grown with 300 ppm K.

### Introduction

Elevated K fertilization during wholesale bedding plant production may reduce irrigation demand as well as the detrimental effects of moisture stress that often occur during retail maintenance and landscape establishment. Work with several agronomic crops (Brag, 1972; Lindhauer, 1985) and woody species (Bradbury and Malcolm, 1977) indicate increasing K rate may reduce transpirational water loss without reducing plant growth. Increasing K rate has also been reported to moderate the influence of moisture stress on gas exchange for several plant species (Berkowitz and Whalen, 1985; Lindhauer, 1985; Pier and Berkowitz, 1987).

Reductions in leaf conductance and transpirational water loss with K rates greater than 300 ppm K have both been reported for salvia (Salvia splendens 'Bonfire') by Eakes, et al. (1989); however, the plants were not subjected to moisture stress to determine the influence of K rate on gas exchange parameters as moisture deficits occur. The objective of this study was to determine the influence of K nutrition on gas exchange, hourly gravimetric water loss, and growth of salvia during moisture stress.

### Materials and Methods

Seed of salvia were sown on 11 Jan. 1988 and glasshouse grown as described by Eakes et al. (1989). Potassium treatments were applied as KCl with each watering at rates of 75, 300, and 600 ppm. Each K solution contained 200 ppm N as  $\text{NH}_4\text{NO}_3$  and 25 ppm P as phosphoric

acid. Treatments were arranged in a randomized complete block design with 16 single-plant replicates for each treatment.

Plants were irrigated at 0545 HR and placed under supplemental lighting provided with 1000-watt high pressure sodium lamps. Levels of photosynthetic photon flux (PPF) were maintained at  $600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  or greater. Net photosynthesis (Pn), transpiration (E), leaf conductance ( $g_1$ ), chamber  $\text{CO}_2$  concentration (CA), and internal  $\text{CO}_2$  concentration (CI) were obtained using the LI-COR Model 6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE). Mean chamber relative humidity, temperature, and  $\text{CO}_2$  concentration were 33 percent, 28 C, 359 ppm, respectively. Water use efficiency (WUE) estimates were calculated by dividing corresponding LI-COR Pn observations by E rates. Mesophyllic resistance to  $\text{CO}_2$  ( $r_m$ ) was determined using the equation:  $r_m = \text{CI}/\text{Pn}$  (Osonubi and Davies, 1980). Gas exchange measurements were taken for each plant in 8 of the 16 experimental blocks every 1.5 hours from 0900 to 1630 HR on 17 Mar. and from 0900 to 1200 HR on 18 Mar. 1988. Hourly plant gravimetric water loss (per unit leaf area) was determined for the remaining eight experimental blocks on the same days that LI-COR gas exchange observations were made as described by Eakes et al. (1989).

To prevent significant losses in total leaf area during  $\psi_1$  observations with the pressure chamber (Scholander et al., 1965), three plants per treatment were randomly selected for readings at 0630, 1100 and 1630 HR on day one and 0630 and 1100 HR on day two of the experiment. Plants were harvested following final physiological observations to determine shoot dry weight and total leaf area.

Data were subjected to analysis of variance (ANOVA) and mean comparisons were made using Tukey's studentized range test (HSD) at the 5 percent level. Gas exchange and plant water status data were analyzed within each observation time.

### Results

Greater  $E$  (Fig. 1) and  $g_1$  (Fig. 2) were observed from 1330 to 1630 HR on day one for plants grown with 75 ppm K. There were no differences in  $E$  and  $g_1$  during day one between plants grown at 300 and 600 ppm K. Both  $E$  and  $g_1$  were lower on day two compared to day one regardless of K rate and declined over time. Plants grown with 600 ppm K maintained higher  $E$  and  $g_1$  than plants grown with 75 ppm at observation times 1030 and 1200 HR on day two.

Hourly gravimetric water loss was lower throughout most of day one for plants grown with K rates of 300 and 600 ppm compared to 75 ppm (Fig. 3). Maximum hourly gravimetric water loss observations, regardless of K rate, occurred from 1200 to 1300 HR on day one. Peak hourly gravimetric water loss measurements occurred at 0900 HR on day two for all three K rates and marked the time that no further differences existed among K treatments during the remainder of the experiment.

$P_n$  throughout day one was greatest for plants grown with 75 ppm K compared to other K rates, peaking at  $20.9 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at 1330 HR (Fig. 4). Plants receiving 300 and 600 ppm K responded alike, reaching a comparatively reduced peak of  $13.9 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at 1200 HR. Day two  $P_n$  observations provided sharp contrast to those of day one;

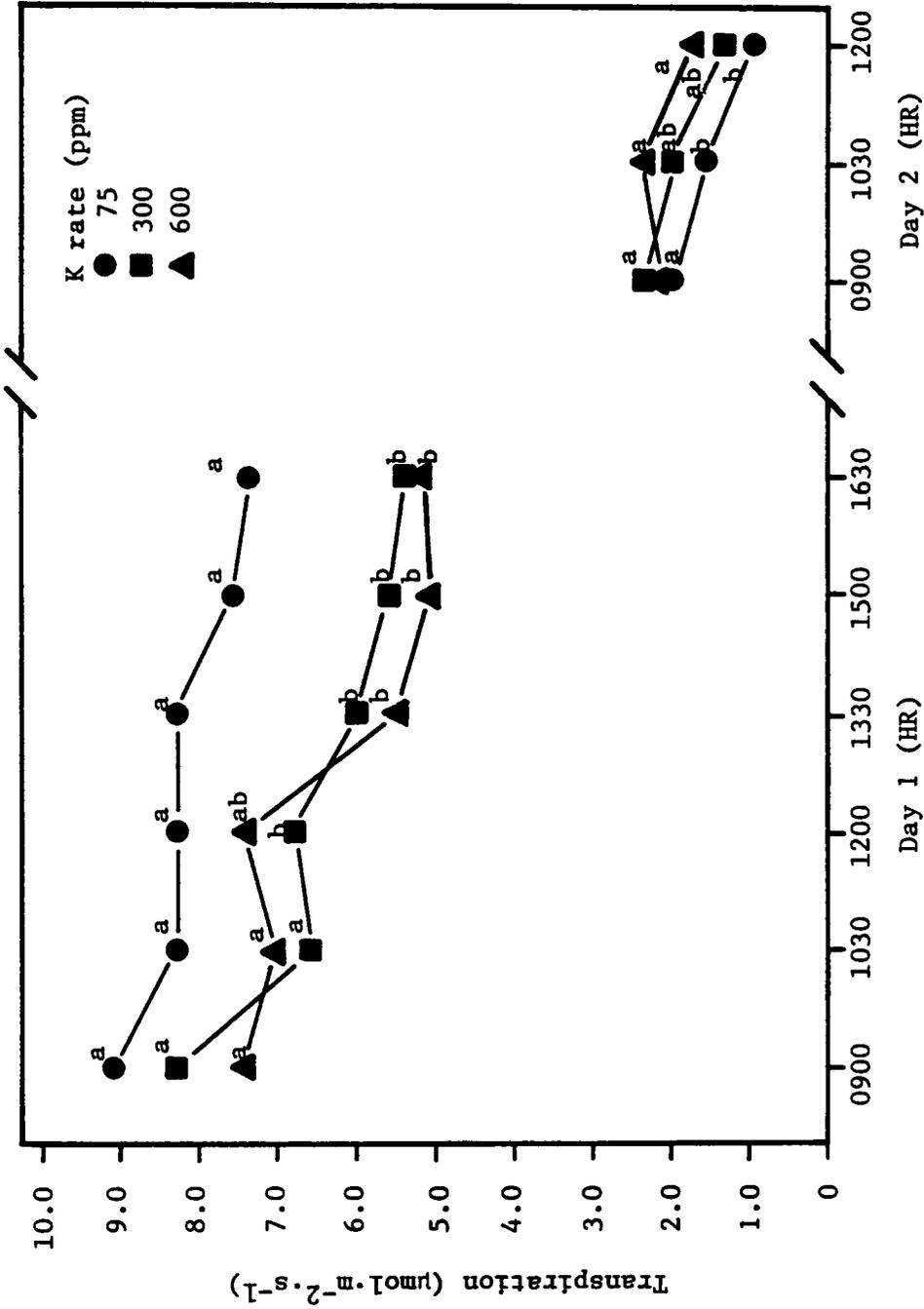


Fig. 1. Transpiration of *Salvia splendens* 'Bonfire' as influenced by potassium (K) rate during the onset of moisture stress. Treatment means are separated within observation times by Tukey's studentized range (HSD) test at the 5% level.

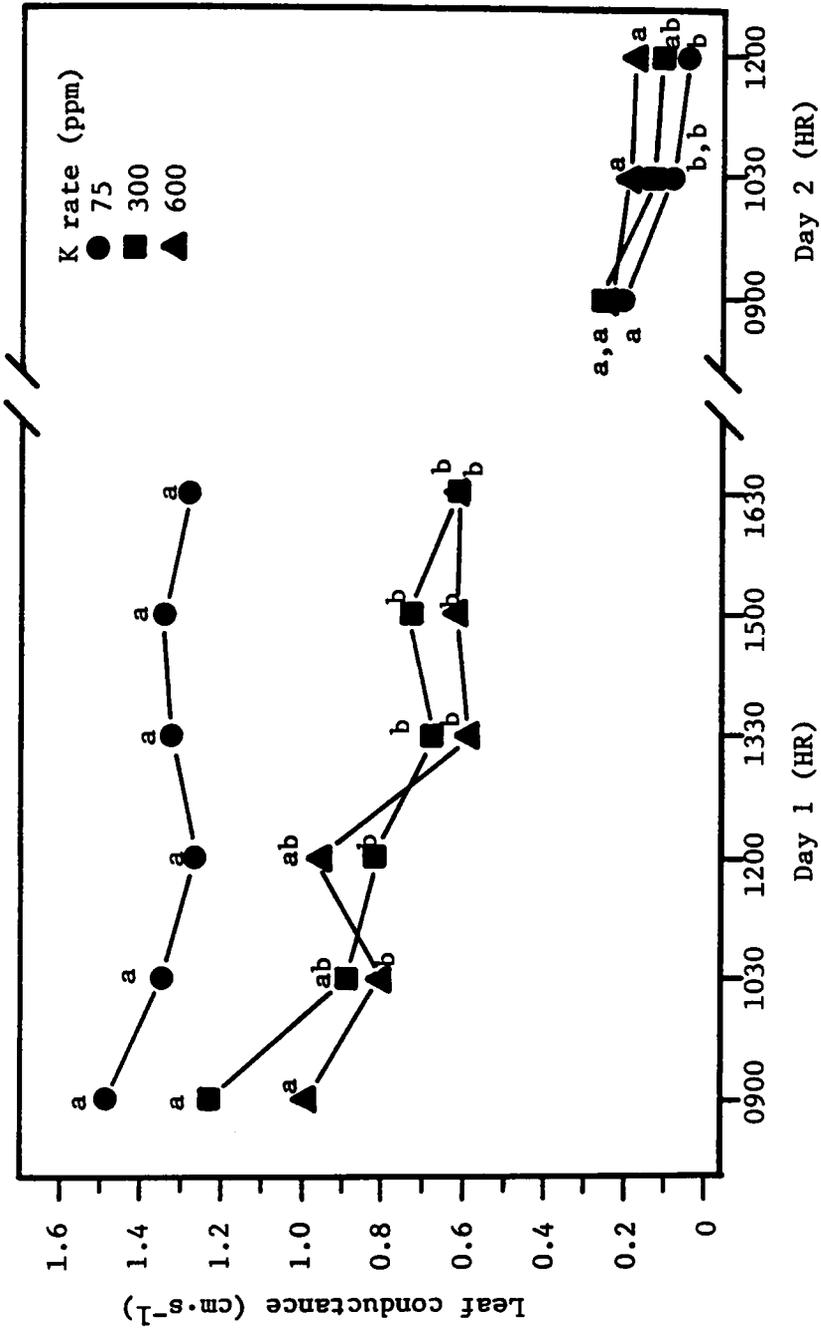


Fig. 2. Leaf conductance to water vapor of *Salvia splendens* 'Bonfire' as influenced by potassium (K) rate during the onset of moisture stress. Treatment means are separated within observation times by Tukey's studentized range (HSD) test at the 5% level.

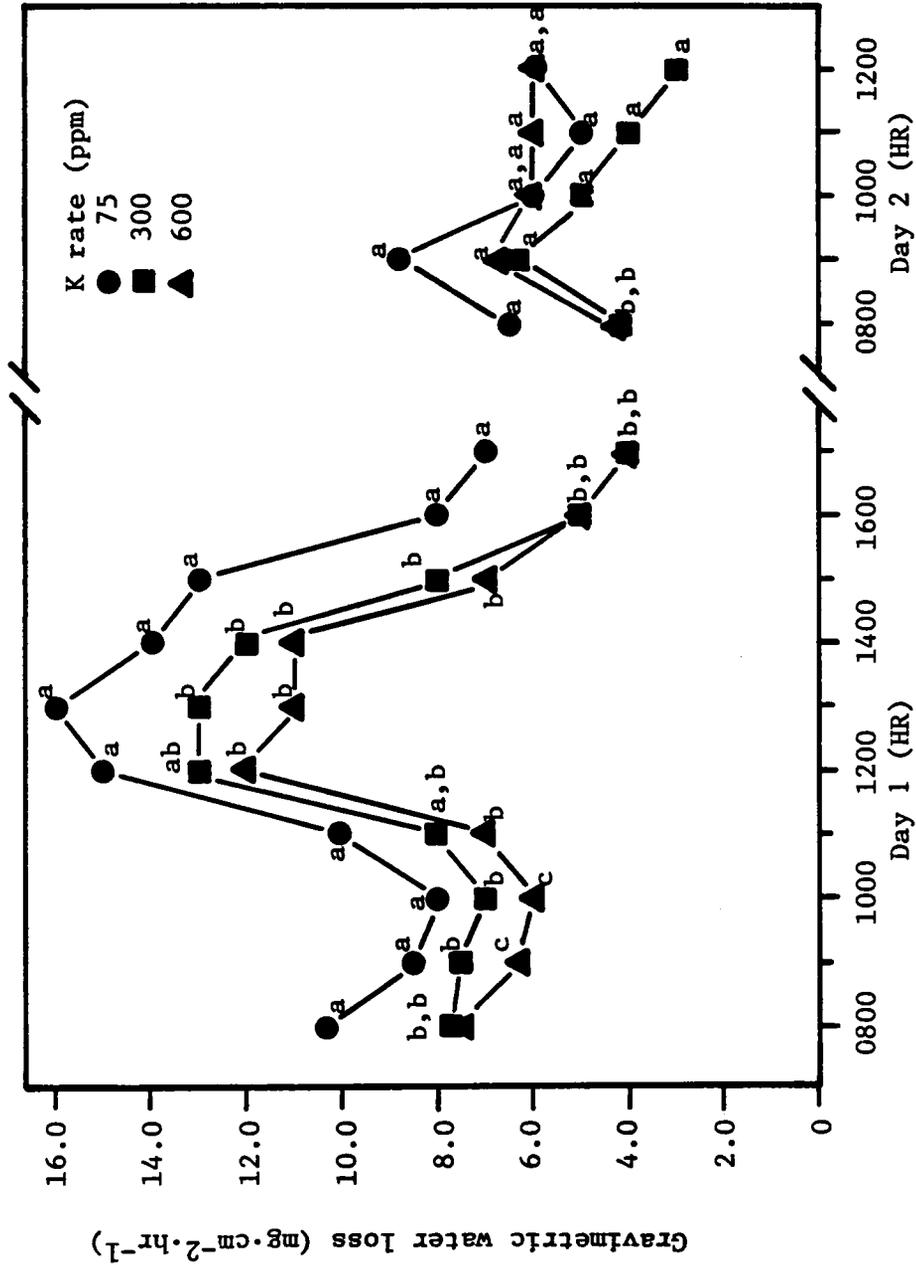


Fig. 3. Hourly gravimetric water loss of *Salvia splendens* 'Bonfire' as influenced by potassium (K) rate during the onset of moisture stress. Treatment means are separated within observation times by Tukey's studentized range (HSD) test at the 5% level.

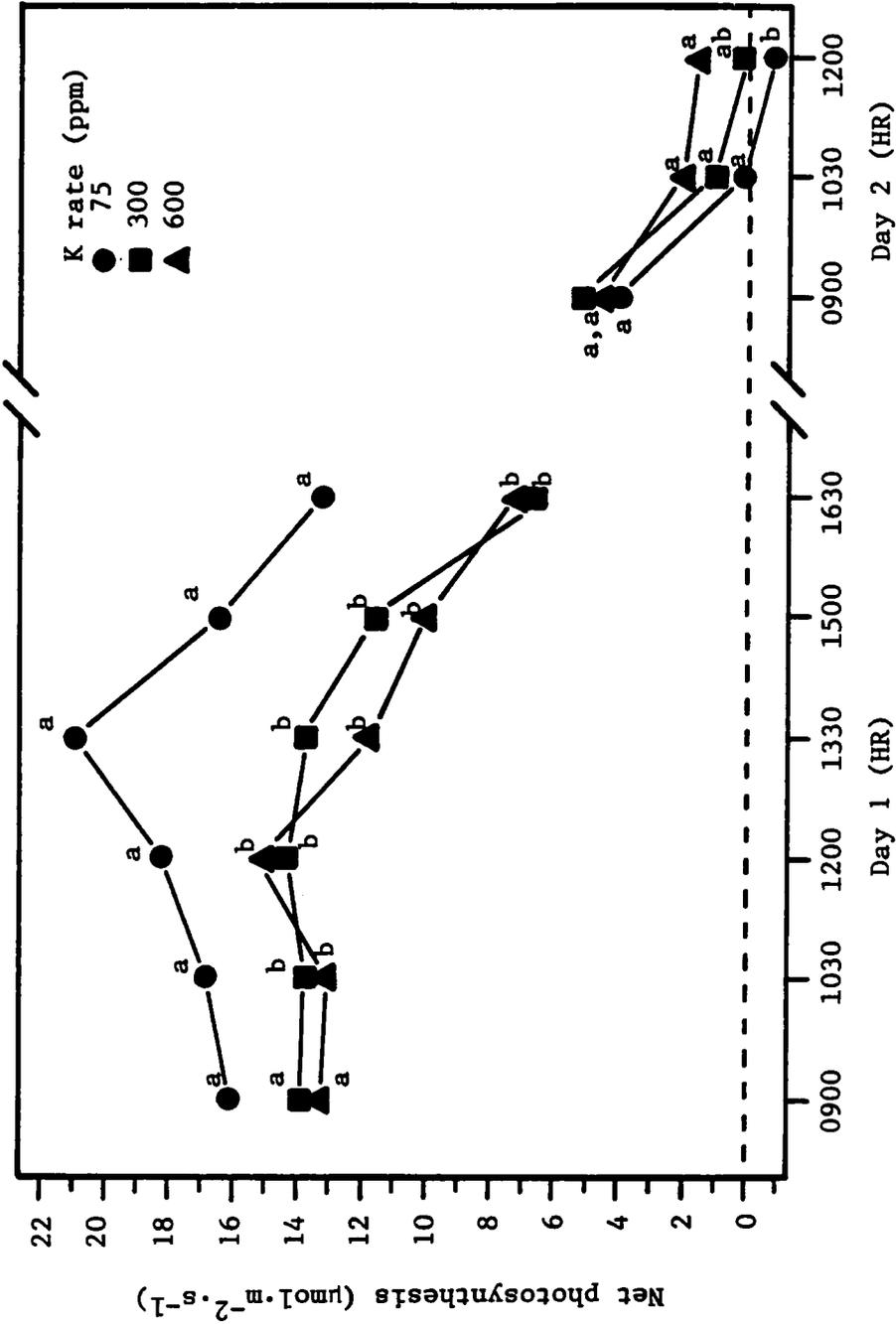


Fig. 4. Net photosynthesis of *Salvia splendens* 'Bonfire' as influenced by potassium (K) rate during the onset of moisture stress. Treatment means are separated within observation times by Tukey's studentized range (HSD) test at the 5% level.

initial measurements continued the decline of the previous day and final observations showed a greater Pn for plants grown with 600 ppm K than those grown with 75 ppm K. Few differences in  $r_m$  were detected between K rates for the two day study (data not shown).

WUE was affected by K treatments only for the final observation on day one and two (Fig. 5). At 1630 HR on day one, 75 ppm K plants had the highest WUE estimates; at 1200 HR on day two the 600 ppm K plants were the most efficient.

Potassium rate did not influence  $\psi_1$  during the duration of the study (Table 1). However at 1100 HR on day two, plants grown with 75 ppm K and several receiving 300 ppm K were visibly wilted having mean  $\psi_1$  of -0.84 and -1.08 MPa respectively; none of the 600 ppm K plants exhibited visible wilt with a mean  $\psi_1$  of -1.09 MPa.

Total shoot dry weight and leaf area were greatest for plants grown with 300 ppm K (Table 2).

### Discussion

Lower E and hourly gravimetric water loss for K rates of 300 and 600 ppm during day one of this study, while plants were well watered, indicate increasing K rate should improve tolerance of salvia to moisture stress through dehydration avoidance. Reductions in E with increasing K rate have previously been reported for salvia (Eakes et al., 1989), as well as spruce (Bradbury and Malcolm, 1977) and several crop species (Brag, 1972, Lindhauer, 1985), but not all reports agree. Others have reported increases in E with increased K rates applied to corn (Koch and Estes, 1975, Peaslee and Moss, 1968) and

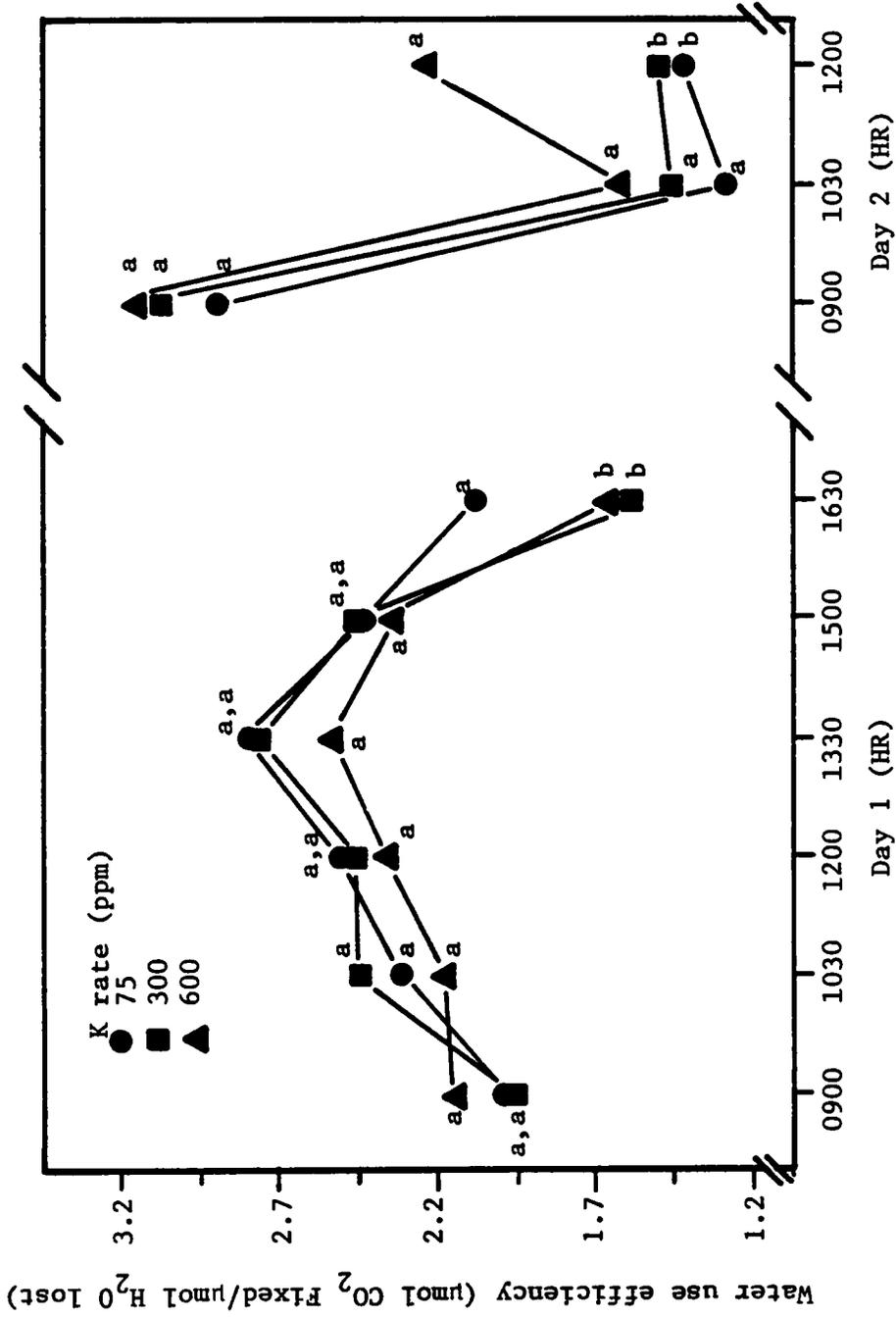


Fig. 5. Water use efficiency estimates of *Salvia splendens* 'Bonfire' as influenced by potassium (K) rate during the onset of moisture stress. Treatment means are separated within observation times by Tukey's studentized range (HSD) test at the 5% level.

Table 1. Leaf water potential of Salvia splendens 'Bonfire' as influenced by potassium (K) rate during the onset of moisture stress.

K rate (ppm)	Leaf water potential (-MPa)				
	Day 1 (HR)			Day 2 (HR)	
	0630	1100	0430	0630	1100
75	0.17a <sup>z</sup>	0.59a	0.49a	0.19a	0.84a <sup>y</sup>
300	0.13a	0.47a	0.34a	0.24a	1.08a
600	0.24a	0.54a	0.47a	0.21a	1.09a

<sup>z</sup>Means separated within columns by Tukey's studentized range (HSD) test, 5% level.

<sup>y</sup>Plants grown with 75 and 300 ppm K showing visible wilt.

Table 2. Shoot dry weight and total leaf area of Salvia splendens 'Bonfire' as influenced by potassium (K) rate.

K rate (ppm)	Shoot dry wt. (g)	Total leaf area (cm <sup>2</sup> )
75	4.8b <sup>z</sup>	1280b
300	5.6a	1520a
600	4.5b	1290b

<sup>z</sup>Means separated within columns by Tukey's studentized range (HSD) test, 5% level.

pigeon pea (Rao and Rao, 1983). Consequently, the effect that K rate has on transpirational water loss may be species dependent.

Similar reductions in  $g_1$  as compared to E at any given observation time during day one indicate reductions in water loss with increasing K rates were probably due to stomatal changes. Although anatomical changes were not determined in this study, reductions in  $g_1$  during day one with increasing K rates may have been facilitated by reductions in stomatal aperture and/or density per unit leaf area. Brag (1972) found wheat grown with high K rates had lower E and attributed these reductions to smaller stomatal apertures and fewer stomata per unit leaf area compared to plants grown with lower K rates. However, in a similar study using Sitka spruce, Bradbury and Malcolm (1977) observed reductions in E when seedlings were placed under high K nutrition levels. Reductions in E occurred too rapidly to be explained by anatomical changes and were therefore attributed to changes in stomatal aperture. Reductions Pn as K rate increased on day one may also be due to stomatal changes based on few differences in  $r_m$  with K rate.

Gas exchange observations on day two were much lower than those observed for day one despite evidence that plants were able to fully rehydrate overnight regardless of K rate. This is indicated by similar  $\psi_1$  at 0630 HR on day two compared to those observed for plants at the same time on day one. E and Pn were dramatically reduced on day two by 0900 HR, regardless of K rate. Based on these observations, and the fact that hourly gravimetric water loss increased from 0800 to 0900 HR regardless of K rate suggests that moisture became

limiting at or near 0900 HR on day two causing the onset of stomatal closure for plants in all three K rates. Stomatal closure due to moisture deficits is further supported by reductions in  $g_1$ .

Although  $P_n$  was lower on day two for all K rates than those observed during day one, plants grown with 600 ppm K were able to maintain higher  $P_n$  to similar  $\psi_1$  than plants grown with 75 ppm K during final observations at 1200 HR. Our data indicate that greater  $P_n$  for 600 ppm K plants was due to higher  $g_1$  than plants grown with 75 ppm K. Lindhauer (1985) using sunflower also observed plants grown with high K rates maintained greater  $g_1$  during the onset of internal moisture deficits than low K plants. Furthermore he attributed this acclimation partly to increased leaf osmotic and turgor potentials allowing stomata to stay open despite low soil moisture levels. *Salvia* has also been shown to osmotically adjust to increasing K rates allowing greater turgor potentials at low  $\psi_1$  (Eakes et al., 1989), which may explain the photosynthetic acclimation to low  $\psi_1$  observed for high K rates in this study.

Potassium rate had little effect on WUE in spite of the fact that K rates altered  $P_n$  and E throughout the two day experiment. Similar responses in  $P_n$  and E for plants grown with each K rate throughout the majority of this study appear to be responsible for few differences in WUE being observed between K rates. In contrast, previous work with spruce demonstrated an increase in WUE when grown with high K rates (Bradbury and Malcolm, 1977).

Total shoot dry weight and leaf area were greatest for plants grown with K rates of 300 ppm (Table 3). Previous work with *salvia*

also demonstrated greatest dry matter yield to occur at K rates of 300 ppm, but in that same study total leaf area increased linearly as K rate increased to 600 ppm (Eakes et al., 1989). Differences in plant growth between this study and previous work with salvia may be due the time of year each were performed. Our experiment took place in the spring of the year while earlier work was performed during the fall.

Results of this study indicate increasing K rates may improve the tolerance of salvia to moisture stress through stomatal changes which reduce transpirational water loss on a unit leaf area basis, and through changes allowing Pn to continue at similar  $\psi_1$ . However, at the 600 ppm K rate it appears that these improvements in moisture stress tolerance are accomplished at the expense of plant growth. Reductions in water loss per unit leaf area with 600 ppm K were not any greater than those observed for 300 ppm K plants and consequently use of K rates beyond 300 ppm K may not prove beneficial.

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## Chapter V

### Final Discussion

Moisture stress following wholesale production is probably the single most important factor contributing to the decline of bedding plant quality in the retail market and landscape. Currently recommendations to growers for maintenance of post-production quality of bedding plants generally include reducing moisture, nutrient, and temperature levels during the final weeks of production to "harden off" plants before leaving the wholesale growing area (Nelson, 1985). Despite common use of these cultural practices by growers, documentation is not available to support their use and more work is needed to find better ways to improve maintenance of plant quality after leaving the wholesale greenhouse. Consequently the objective of this research was to determine the influence of moisture stress conditioning (MSC) and K rate on physiological parameters related to moisture stress tolerance of the bedding plant salvia (Salvia splendens 'Bonfire').

Net photosynthesis (Pn), transpiration (E), and hourly gravimetric water loss were reduced by MSC under well watered conditions. These reductions appear to be caused by stomatal changes based on similar reductions in leaf conductance ( $g_1$ ) during this period without changes in mesophyllic resistance to CO<sub>2</sub> ( $r_m$ ). However; as leaf water potentials ( $\psi_1$ ) dropped over time, MSC plants maintained Pn, E,

$g_1$ , and hourly gravimetric water losses to lower  $\psi_1$  than controls. Maintenance of turgor, apparently due to osmotic adjustment, during these reductions in  $\psi_1$  by MSC plants facilitated the continuation of these physiological processes essential for plant growth and development. Although the process of MSC consistently reduced dry matter yield during production, water use efficiency (WUE) was increased regardless of plant water status following completion of MSC cycles.

Increasing K rate also reduced Pn, E, and hourly gravimetric water loss under well watered conditions. Reductions in E and hourly gravimetric water loss with high K rates appear to be due to stomatal adaptations based on lower  $g_1$ . Plants grown with 300 ppm K produced leaf areas that were 16 and 15 percent greater than 75 and 600 ppm K plants, respectively. Despite this greater leaf area for 300 ppm K plants, moisture became limiting at approximately the same time for both 75 and 300 ppm K plants. Plants grown with 600 ppm K maintained greater Pn, E,  $g_1$ , and hourly gravimetric water loss at similar  $\psi_1$  compared to 75 ppm plants indicating photosynthetic acclimation to low  $\psi_1$  for the higher K rate.

These physiological adaptations for plants grown with MSC and increasing K rate may be due to osmotic adjustment. Both exposure to MSC and increasing K rate caused foliar osmotic adjustment and maintenance of positive cellular turgor potentials at  $\psi_1$ . Although increased foliar K concentrations indicate K was a major solute involved in osmotic adjustment, these osmotic changes appear to be due osmotic stress caused by high medium soluble salt concentrations.

Results of the research indicate MSC and increasing K rate may improve the water conservation of salvia through stomatal changes which reduce transpirational water loss on a per unit leaf area basis. Metabolic changes which allowed Pn to continue at  $\psi_1$  also resulted. However, before recommendations can be made for use of MSC and increasing K rate at the commercial level, further investigation is required. Areas of importance would include:

- 1) determining ways for growers to prevent damage from excessive moisture stress and soluble salt levels;
- 2) evaluating other bedding plant species;
- 3) evaluating field performance under limited moisture conditions.

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