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Accelerating Production of Slow-Growing Intermountain West Native Plants by Modifying Their microclimate

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ACCELERATING PRODUCTION OF SLOW-GROWING INTERMOUNTAIN WEST NATIVE PLANTS BY MODIFYING THEIR MICROCLIMATE

by

Sam Miller

A thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

Plant Science

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2011
ABSTRACT

Accelerating Production of Slow-Growing Intermountain West Native Plants by Modifying Their microclimate

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Sam Miller, Master of Science
Utah State University, 2011

Major Professors: Dr. Roger Kjelgren, and Dr. Heidi Kratsch
Program: Plants, Soils, and Climate

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Sam Miller
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In the western United States (US), water shortages are a recurring problem (Barnett et al., 2004). The western US is largely arid; for example, Utah and Nevada receive the least amount of annual precipitation of any states in the US (UDWR, 2007). Despite little available water, per capita water use in these states is the highest in the nation (UDWR, 2007). Historically, rivers and runoff impounded in dams have been able to support societal water needs, but significant changes in the western US water cycle are occurring due to increased levels of greenhouse gases accelerating climate change (Madrigal, 2008). Also, much of the precipitation in the western US occurs in the form of snow, but as winter temperatures rise, less snow accumulation occurs (Mote et al., 2005). This results in less runoff that can be collected by dams and reservoirs. With the combination of high demand and human-influenced climate change, water shortages are now more likely to occur than ever before (Vorosmarty et al., 2000).

As the population in the western US continues to grow, water shortages will become greater. Urban areas such as Las Vegas and Los Angeles are already dealing with water shortages (Moran and Hinman, 2007). Las Vegas is almost completely dependent on the Colorado River for water, but recent decreased flows of the river are forcing the city to seek additional water supplies elsewhere. The Southern Nevada Water Authority has proposed a $2 billion pipeline that will pump in water from 250 miles away in southwestern Utah. Without supplemental water, Las Vegas is at risk of running out of water in the near future (Lawrence, 2007).
In urbanized areas within the Intermountain West (IMW), 30%-70% of the yearly municipal water consumption goes toward irrigation of urban landscapes (Mee et al., 2003). This high water use for landscape irrigation is largely due to using plants that are not adapted to the arid conditions of the western US. The vast majority of urban landscapes consist of traditional landscape plants such as cool-season turfgrass and non-drought tolerant trees and shrubs. Landscapes with traditional plants often require a substantial amount of supplemental water in this climate. Specifically, a great percentage of this water is being used to irrigate lawns (UDWR, 2009). Because landscape water accounts for such a large percentage of the water used in the West, water suppliers are trying to educate and encourage the application of low water landscaping as an alternative to conventional landscapes. The main focus of low water landscaping is to use plant species that can potentially require significantly less water by replacing turfgrass with low water use trees, shrubs, grasses and perennials.

Applying the principles of low-water landscaping to urban landscapes can eventually result in substantially lower water use (UDWR, 2009). Experiments have shown an average water savings of 30% for those who converted from turf to xeriscape (Sovocool, 2005). Species native to the deserts of the IMW region are logical for use in low-water landscaping. Native species are great choices because of their ability to adapt to abiotic stresses (Ochoa et al., 2010). Native IMW species have evolved adaptations to intense heat, sunlight, drought, and little or no nutrients, allowing them to thrive in the deserts of the IMW, with little water and infertile soil (Mee et al., 2003). However, designing and installing a low-water landscape using native IMW species is difficult, due to the lack of availability at nurseries. Some of the most attractive and drought-adapted
native trees and shrubs grow so slowly that achieving a marketable size takes many times longer than growing more conventional species. It is simply not cost-effective for growers to produce most of these slow-growing natives, so they usually choose to grow faster growing and less drought-tolerant conventional plant material. Plants native to the IMW grow so slowly because of their adaptations to their arid habitat. These plants tend to have small leaf size, with high LMA. They also tend to allocate a large percentage of resources to building root mass rather than shoots and they often have well-regulated stomata.

The purpose of this experiment was to determine whether the growth of two slow-growing woody natives can be accelerated by manipulating the growing environment. Specifically, root zone temperature moderation by PIP and leaf temperature moderation by shading, were tested. These experiments allowed us to determine whether growth rates can be increased and determinate growth inhibited, or if slow growth is simply independent of environmental stimulus.

The study plants were, therefore, tested to determine the degree of plasticity they possess. Phenotypic plasticity is the ability of an organism to change in response to its environment. A single genotype can express different phenotypes depending on different environments (Sultan, 2003). Plants generally have much greater plasticity than animals, yet each plant species is plastic to varying degrees. Even within the same habitat, similar plants can show different degrees of plasticity. Slow-growing species are commonly much less plastic than fast-growing species. However, it has been shown that biomass allocation between leaves and roots is actually more plastic in slow-growing plants when plants were grown under contrasting temperatures (Atkin et al., 2006). Because greater
leaf growth has been realized at contrasting temperatures for slow-growing species, it makes sense to manipulate the growing microclimate to control temperature, in hopes of increasing above-ground growth.

Two slow-growing native species with high landscape potential were used to test our hypothesis: single-leaf pinyon pine (*Pinus monophylla*) and Utah holly (*Mahonia fremontii*). *Pinus monophylla* is a predominant tree species in the low montane foothill regions of the Great Basin, found as a co-dominant with Utah juniper (*Juniperus osteosperma*). *Pinus monophylla* ranges from southern Idaho and western Utah, through most of Nevada, and is also present in sporadic populations through southeastern California and northern Baja California, as well as Arizona and New Mexico (Zouhar, 2001). *Mahonia fremontii* is a broadleaf evergreen shrub typically found growing in pinyon-juniper and cool desert shrub plant communities (Mee et al., 2003). It tends to grow on rocky slopes and benches throughout much of the IMW region in Utah, Colorado, New Mexico and Arizona, usually between 1200 m and 2800 m. Both species show great potential for low watering landscaping due to their attractiveness and low water usage, and will be great assets to the nursery industry if production can be accelerated.

The study species were grown from wild collected seed. The *P. monophylla* seed was collected from a highly desirable population with incredibly blue foliage located in the Raft River Mountains of Box Elder County in Northern Utah. The seed source was at an elevation of approximately 1615 m, growing in fast draining sandy loam soil. The *M. fremontii* seed was collected in Buckhorn Wash of the San Rafael Swell in central Utah,
at an elevation of approximately 1664 m. This seed source was growing in fast draining soil in a sandy outwash.

Objectives

The purpose of this thesis research was to determine whether the growth of slow-growing woody native species can be accelerated by manipulating the growing environment. Specifically, it will be determined if pot-in-pot (PIP) moderates root zone temperatures and if shading moderates leaf temperature, and if the resultant effects lead to increased growth. These experiments will determine whether growth rates can be increased and determinate growth inhibited, or if slow growth is simply independent of environmental stimulus.
CHAPTER 2
LITERATURE REVIEW

The slow-growing nature of many native Intermountain West (IMW) woody species is most likely due to drought adaptation. These species allocate much more carbon into root growth because deep-rooted plants are able to maintain higher leaf water potential (Bucci et al., 2009). Species adapted to drought cannot afford to invest carbon into aboveground growth without having a root system that can extract a sufficient supply of soil water. This is accomplished via deep, extensive root systems that allow these plants access to more water. In addition to deep roots, many species have very wide spreading horizontal roots (Stern, 2003). This allows the plants to take advantage of any precipitation that may occur, and also acts to limit the ability of any competing plant to take root. This is the reason for the relatively wide spacing of plants in these communities (Campbell and Reece, 2002).

Additionally, many drought adapted species have above-ground adaptations. To cope with low water, many species have evolved small leaf size, as well as small overall plant size, to reduce transpiration (McDonald et al., 2003). This is a key adaptation to limited water supplies. As precipitation decreases, less leaf area can be supported. Small leaf size requires less transpiration to regulate leaf surface temperature. Conversely, larger leaf surfaces heat up more rapidly and require more transpiration to maintain non-damaging leaf temperatures. Thus, many high desert native plant species have leaves that are less than an inch across (Mee et al., 2003).

Another key adaptation is the blue-green foliage of many of these plants. Blue foliage allows the leaves to reflect more of the high-energy blue band solar radiation and
reduce temperature (Mulroy, 1979). Most drought tolerant plants also have very well regulated stomatal openings. Many species have stomata that are sunken deep within the leaf surface and leaf hairs, both of which act to reduce wind speed, increase boundary layer, and prevent desiccation (Stern, 2003). These traits all help to reduce transpiration by limiting the conductance of water vapor from leaves. However, with the stomata closed, the plants cannot photosynthesize and do not acquire additional carbon necessary for growth.

In general, these adaptations cause slow top growth by reducing carbon allocation to leaves and stems. For instance, the large investment in root growth typically translates to less leaf and stem growth. Additionally, the leaves that these arid habitat plants produce are commonly leathery and have high leaf dry mass per unit area (LMA). Typically, high LMA species have higher leaf tissue densities (Poorter et al., 2009). Building high LMA leaves requires more resource investment per unit leaf area, which also tends to result in slow growth.

The drought adaptation characteristics that limit stomatal conductance \( (g_s) \) also limit photosynthesis. These physiological traits, coupled with determinate growth, which is likely triggered by environmental factors, result in plants that grow very little each year. As a result, IMW native woody species tend to grow for only a short time in the spring (Stern, 2003). Signals such as drought and hot dry air act to trigger growth suppression during the onset of summer (Oleksyn et al., 1998). High temperatures have been shown to be a major limiting factor in plant growth, especially in containerized stock (Harris, 1967). The temperature of the root zone in containerized plants can get extremely high in the heat of the summer. Temperatures in excess of 48°C are found
near the sides of exposed containers. These high temperatures will often lead to death in root tissue. In fact, a study using Loblolly pine (*Pinus taeda*) found that maximum root growth occurred at temperatures between 21-27°C, with growth reduced as much as 90% at 35°C (Barney, 1947). This same study found that a number of conifers were killed in only a few hours at 47°C in the root zone. In a study performed at the Oklahoma Agricultural Experiment Station, it was shown that growing plants under shade can help to decrease root loss by decreasing heat in the root zone of containerized plants (Whitcomb and Mahoney, 1984).

By manipulating the growing environment and decreasing the intensity of extreme environmental signals it should be feasible to extend the growing season and allow for more growth during the hottest parts of summer. Several management options are available to moderate environmental extremes, the first and most obvious of which is irrigation and nutrients. Providing water as needed prevents drought stress in nursery grown native species, and providing nutrients prevents potential deficits. However, supplemental water and nutrients alone do not appear to stop mid-summer growth suppression. These slow-growing natives still show greatly reduced and highly determinate growth in the late spring and don’t start growing again until fall when temperatures are cooler.

High temperature coupled with high vapor pressure deficits and low humidity are potentially limiting to nursery production in a high desert environment. These factors lead to increased transpiration and could contribute in triggering the determinate growth pattern. Management options to control temperature include the use of pot-in-pot (PIP) production to moderate high root zone temperatures and overhead shading to reduce high
leaf temperatures. The use of PIP production for nursery material can encourage significantly greater growth by decreasing root zone temperatures of containerized stock (Ruter, 1993). It also reduces irrigation needs, lessens heat stress to the root zone during the summer, and minimizes root-zone temperature fluctuations in the winter (Owings, 2005). Similarly, shading of production plants decreases the intensity of solar irradiation, thus decreasing leaf temperature. It may also work to limit the intensity of hot dry winds by providing additional protection which decreases vapor pressure deficits and helps alleviate growth suppression triggers.

Two slow-growing species with high landscape potential in the IMW, are single-leaf pinyon pine (*Pinus monophylla*) and Utah holly (*Mahonia fremontii*). Both species were individually investigated in this study.

*Pinus monophylla* is a predominant tree species in the low montane or foothills of the Great Basin, found as a co-dominant with Utah juniper (*Juniperus osteosperma*). *Pinus monophylla* ranges from southern Idaho and western Utah, through most of Nevada, and is also present in sporadic populations through southeastern California and northern Baja California, as well as parts of Arizona (Zouhar, 2001). Colorado pinyon (*Pinus edulis*), also called common pinyon, is a similar pine species that grows to the east of *P. monophylla*’s range. *Pinus edulis* is a closely related, yet distinct, two-needled pinyon species found throughout the southeastern section of the IMW and the Colorado Plateau (Lanner, 1981). Although both pinyons are very drought-hardy, summer rain is much more common in the habitat of *P. edulis*, and as a result *P. monophylla* is likely more drought tolerant.
Utah holly (*Mahonia fremontii*) is a broadleaf evergreen shrub typically found growing in pinyon-juniper and cool desert shrub plant communities (Mee et al., 2003). It is commonly found on rocky slopes and benches throughout much of the IMW region in Utah, Colorado, New Mexico and Arizona, usually between 1200 m and 2800 m. It is related to the common barberry (*Berberis ssp.*) which is often used in more traditional landscapes, yet *M. fremontii* is much more drought tolerant. Another common native species of *Mahonia* is creeping Oregon grape (*Mahonia repens*). *M. repens* is widely available in the trade because it can be produced significantly faster than *M. fremontii*. However, the appearance of the two *Mahonia* species is significantly different. *Mahonia repens* is a small prostrate ground cover, whereas *M. fremontii* is a shrub that averages between 5’-10’ tall (Elmore, 1976). Additionally, *M. fremontii* is likely much more drought tolerant than *M. repens*, which tends to grow in more mesic sites, typically in the shaded understory.

Both *P. monophylla* and *M. fremontii* show great potential for low water landscaping due to their visually attractive appearance and low water usage. According to the USDA forest service, *P. monophylla* grows under more xeric conditions than any other pine in the U.S. (Zouhar, 2001). Average annual precipitation in its habitat ranges from approximately 200 mm to 460 mm, with a mean maximum temperature of 30°C (Meeuwig, 1990). *Pinus monophylla*’s exceptional drought tolerance is probably due, in part, to its unique single needle (Lanner, 1981). *Pinus monophylla* is the world’s only pine with a single needle or leaf per fascicle, an adaptation that is likely advantageous because it decreases the number of stomatal openings. The decrease in stomatal openings lowers the rate of transpiration, thus conserving limited soil water. Also, *P. monophylla*
leaves are more glaucous than those of the closely related *P. edulis*, which should allow it to reflect more high energy blue light (Mulroy, 1979). These drought advantages are most likely what enabled this species to expand its range into the desperately hot and dry regions of the Great Basin.

It is not only these species’ high tolerance for drought that adds value to low water landscapes, but also their aesthetic qualities. *Pinus monophylla* is a relatively small conifer tree with the blue-green foliage characteristic of many desert plants. The appearance of singleleaf pinyon is almost closer to that of a small Colorado spruce (*Picea pungens*) than other more well known pines, although the canopy is usually much broader. The bark is smooth and thin on young trees, becoming deeply fissured and ridged, and up to an inch thick with age (Zouhar, 2001). Mature dominant trees in the wild tend to be between 20’-40’, depending largely on the site quality and genotype (Meeuwig, 1990).

*Mahonia fremontii* is also a highly attractive shrub with great potential as an ornamental. One of the most striking features is its foliage. Each spring, the new leaves come out a purplish red and then turn a vibrant turquoise blue. Abundant yellow flowers, typical of barberries, cover the plant by mid-spring, giving way to dark red berries in the fall. These berries are edible and quite sweet. With such attractive characteristics, this drought tolerant plant should be available in the nursery trade. However, its slow initial growth makes it difficult for economical nursery production.

Both of these slow-growing species would be great assets to low-water landscaping if they could be produced in a more cost and time efficient way. For instance, *P. monophylla’s* growth is so slow that it usually requires 60 years to attain a
height of roughly 2 meters in the wild (Meeuwig, 1990). In cultivation, they can be
grown somewhat faster, but additional production methods for accelerating growth need
to be investigated.
CHAPTER 3
MATERIALS AND METHODS

Experimental Design

The study was conducted at the Utah Botanical Center (UBC) in Kaysville, Utah. The UBC is a research and educational center dedicated to conservation through the judicious use of plants, water and energy resources in the IMW. This study consisted of two separate, but related experiments: traditional above ground and alternative PIP production. Within each above or below ground experiment, containers were arranged in a split plot design with shade as the main block split between randomly assigned species. The study began in the spring of 2009 (after last predicted frost) and continued until the autumn of 2010 (until the first freeze), providing us with two growing seasons worth of data.

The plant material was initially grown in #1 containers in a substrate comprised of 60% bark, 30% fine pumice, and 10% large pumice for 2 years prior to the study. During mid July of 2008, all plants were repotted into #5 containers using the same substrate. This substrate is free-draining and promotes excellent root growth. At the time of transplanting, the *P. monophylla* were between 15-38 cm tall, and the *M. fremontii* were 61-91 cm tall. Each container was top-dressed with approximately 35 grams of 15N-9P-12K slow-release Osmocote Plus ™ fertilizer (Scott’s Company, Marysville, OH, USA). The fertilizer was mixed evenly into the top layer of soil in each pot. Each plant was labeled so that individual growth could be monitored. All plants were well watered and left to establish new roots for the rest of the season, and overwintered in a coldframe for
2008-2009. The experiment started the following spring in April of 2009 when they were replaced outside and the study treatments applied.

In the aboveground, conventional production experiment, containers were placed on a growing pad with weed fabric underneath to prevent weed growth within the study area. The pad measured 13.7 m long by 3.7 m wide. The blocks consisted of both species (*P. monophylla* and *M. fremontii*). Within each block, the *M. fremontii* was placed to the north and the *P. monophylla* to the south to prevent shading of the pines by the taller *M. fremontii*. The two study species were bordered on all sides by additional #5 containers planted with small shrubs in order to emulate the buffering that a container plant is subject to in a typical nursery setting. The blocks that included the treatment and border plants were four containers deep (north to south) and three containers wide (east to west). Each block consisted of twelve containers and was 84 cm by 112 cm in dimension. All containers were densely spaced, touching each other, with the experimental plants in the middle.

Sixteen individual blocks were setup in this exact manner. Individual blocks were randomly selected to receive shade. Half received shade, while the other half served as a control and received full sun. The sixteen individual blocks allowed for eight plants of each species to be under shade and eight in the control group.

Horticultural grade knitted shade fabric was used. It provided 30% shade and was placed 1.2 m above the ground. The shade structure provided overhead and southern aspect protection from sunlight. With this method the plants remained consistently protected throughout the day, as the shade cloth acted to decrease intense sunlight, heat, and desiccating winds. At a 30% light reduction a better growth response should be
measureable, while still maintaining a reasonable non-limiting light level (Kjelgren et al., 2009).

Plant arrangement in the PIP experiment was different and consisted of two rows of a PIP field with the socket pots 1.2 m apart. Each row started with a border plant, followed by both trial species, then another border plant. Each row repeated this pattern to the end of the row, creating blocks that consisted of two trial plants separated by a border plant. The 30% shade fabric was randomly assigned to the PIP blocks, with half shaded and half in the control group. The shade cloth was placed 91 cm above the ground and was attached overhead and at ground level on the south side. The top of the shade cloth was 30 cm lower in the PIP field to compensate for the fact that the 30-cm pots were below the ground. In this way, the cloth was the same distance from the plants as in the aboveground treatment.

The support structure for the shade cloth in the aboveground experiment was built by burying 1.83 m long 4x4 cedar posts in the ground so that 1.2 m of each post was aboveground. The posts were located so that two (91 cm apart) were at each end of the rows and two in the middle of each row. Wire was attached at the top of each 4x4 and ran the length of each row. Also, wire was attached on the bottom of the southern side. The shade fabric was attached to the wires with zip ties, so that they were shaded from both the south and overhead.

The structure for the PIP experiment was built to the same specifications, with a few minor adjustments made to accommodate height differences in the PIP experiment. Specifically, the 4x4’s were only 91 cm high because the pots were in the ground. Also, the 4x4’s were placed 61 cm apart rather than 91 cm, because they only needed to
provide shade to one plant as opposed to a whole group of plants, as in the above ground experiment. Wires running the length of the row were attached to the top of all 4x4’s and the bottom of the southern 4x4’s in each row. The shade cloth was attached to the wires to provide overhead and southern protection.

Maintenance

Treatment plants were irrigated regularly using 3.8 liters/hr Rain Bird® drip emitters. In the early spring, the plants were watered for 45 minutes every third day. In late spring, they were watered for 45 minutes every other day. During the summer, they were watered for 40 minutes everyday. The soil around the PIP plants was well drained, prohibiting standing water, and the irrigation ensured that the plants were well watered during the growing season.

Additional fertilizer was equally applied to all plants each May for both years after the initial repotting in 2008. Approximately 35 g of 15N-9P-12K Osmocote Plus™ (Scott’s Company, Marysville, OH, USA) were worked into the soil around each plant. Other routine maintenance included weed and vegetation control: all weeds were removed as they emerged from pots or around PIP plants. Grass and weeds were mowed and line-trimmed as needed from the ground surrounding the PIP plants. All *M. fremontii* were pruned to a common height of 40 cm and approximately uniform shape in March of 2010, before seasonal growth began. This maintenance was performed because many of the plants had become tall enough to touch the shade fabric, adding a potentially confounding effect. This also allowed the study plants to start growing from a common point and facilitated measurement of treatment effects on growth.
Data Collection

As an integrated indicator of the effectiveness of soil temperature moderation and shading, the treatment plants were measured for height, width, trunk diameter, and average shoot elongation at the beginning of the experiment in May 2009, just after being placed in the field. The same measurements were then taken again after each growing season. Shoot elongation was the key measurement used to assess the integrated effect of shade on growth.

To assess the direct environmental impact of shading and PIP production, temperatures of the treatment plants’ leaves, container rims, and surface soil were measured for each replicate using an Infrared Temperature Sensor (model SI-111, Apogee Instruments, Logan, UT, USA). These measurements were collected on 15 July 2009 between 12:00 PM and 1:00 PM. Every plant in the study was measured twice and an average value was obtained. The measurements were made by aiming the sensor at the object being measured from directly above.

Using a leaf porometer (model SC-1, Decagon Devices, Pullman, WA, USA), stomatal conductance ($g_s$) was collected. The measured $g_s$ allowed us to determine if the shade protection increased $g_s$ by limiting triggers that lead to stomatal closure. Related to photosynthetic measurement, $g_s$ is representative of the gas exchange rate for water vapor, and can be used to infer the degree of photosynthetic activity.

Only $g_s$ data for *M. fremontii* was collected, as the narrow, rounded pine needles of *P. monophylla* did not allow for effective measurement. The $g_s$ was measured approximately once a week during midday from early July through the first of September in 2009. Measurement was started a month earlier in 2010, and ran from mid June until
the end of August. The $g_s$ was measured from early morning to evening on 12 July 2010 to determine the pattern of stomatal opening throughout the entire day.

To measure the impact of shading and root temperature moderation on the physiology of treatment plants, photosynthesis was measured with a Li-Cor 6400 IRGA gas exchange system (Li-Cor, Lincoln, NE, USA). The Li-Cor 6400 was also used to determine light response curves for representative treatments. Both photosynthesis and light response tests were conducted in the summer of 2010, on both species in the pot-in-pot study. Photosynthesis measurements were collected on 31 August 2010 for both species. *Pinus monophylla* was measured between 9:30am and 10:30am. *Mahonia fremontii* was measured between 10:30am and 11:30am. Four sun and four shade plants were measured for both species. The light response data was collected on 3 August 2010. Again, four sun and four shade plants were measured for both species.

Leaf surfaces and cross sections of each species were imaged with a scanning electron microscope (SEM) at the end of the second year, to determine if any morphological differences were evident between the treatments and species as a result of shade. The images allowed us to analyze any possibly unique physical attributes the leaves of these species possess in order to deal with their harsh environments. Ten equal sized leaf samples were taken from both full sun and 30% shade treatments for each species. The leaf samples were immediately placed in a solution of formalin alcohol acetic acid (FAA) and left for 24 hours. This was followed by a graded dehydration series to 100% ethanol. The samples were then dried using a critical point dryer (Samdri-PVT-3D, Tousimis, Rockville, MD, USA), after which the samples were then sent to the lab at Utah State University to be imaged with the SEM. The SEM images from both
plants were compared and contrasted to SEM images of other similar plants. *Pinus monophylla* was compared with three other pine species (*Pinus edulis*, *P. nigra*, and *P. flexilis*). *Mahonia fremontii* was compared with *Shepherdia rotundifolia* and *Eriogonum corymbosum*. SEM samples for these plants were produced using the same method described above.

Statistical analysis was performed using Statistix 9.0 (Analytical Software, Tallahassee, FL, USA). Growth, $g_s$, and photosynthesis were analyzed using a linear model one-way analysis of variance (ANOVA) for a completely randomized design to determine if there was a statistically significant difference between shade and full sun treatments for both aboveground and PIP studies. Light response curves were analyzed separately for each species by fitting to the model $y=a+bx^{0.5}$, where $y$ is photosynthesis in $\mu$mol m$^{-2}$s$^{-1}$ and $b$ is the slope of the curve. Data for shade and sun treatments with four replications were first fitted together, then separately. An F-statistic was calculated from the discrete regression sums of squares (SS) for the sun and shade equations added together, minus the combined regression SS, corrected for the regression degrees of freedom (DF), divided by the sum of the residual SS/DF for the discrete treatments. Sigmaplot 8.0 (Systat Software Inc., Chicago, IL, USA) was used to visually represent growth, stomatal conductance, and light response curves. Graphs were fitted with error bars representative of the standard error of the averages.
CHAPTER 4
RESULTS AND DISCUSSION

Shading with 30% shade cloth produced a statistically significant decrease in pot, leaf, and soil temperature. In the shade, the pots and leaves were approximately 7 °C cooler, and the soil was approximately 5 °C cooler for both species (Table 1). There were no significant differences between the leaf temperatures of the two species. *Mahonia fremontii* leaves are usually greater than 1 cm, while *P. monophylla* leaves are between 1-2mm wide, but both measured at the same temperature of approximately 35 °C in the shade and approximately 39 °C. Typically, larger leaf surfaces become hotter than smaller ones (Campbell and Reece, 2002). The highly glaucous nature and sharp lobes of *M. fremontii* leaves are likely the reason that they are able to remain the same temperature as a much smaller leaf. Additionally, the pots were much hotter than the leaves, further attesting to the importance of blue foliage in reducing temperature. However, the soil surfaces were cooler than the leaves. The soil surfaces, which were moist when measured, were evaporation cooled, suggesting that the plants leaves were not transpiring at rates great enough to lower temperatures to that of the soil.

It is, however, the differences between the shade and full sun treatments’ temperature that was most important in our effort to overcome the determinate growth habit. The significant decrease in temperature for leaf, pot, and soil under shade provided a less hostile growing environment, which had a positive effect on plant health, further evidenced by our additional findings.

The $g_s$ data of *M. fremontii* confirmed our hypothesis that these plants can have higher $g_s$ under shade than full sun. This was evident in 2009, when $g_s$ was significantly
Table 1. Surface temperature (°C) comparisons of 30% shaded versus full sun *Mahonia fremontii* and *Pinus monophylla*. Measurements include the rim of the containers (Pot), the surface of the leaves (Leaf), and the surface of the soil (Soil). Measurements were made using an SI-111 Infrared Temperature Sensor (Apogee Instruments, Logan, UT, USA). ** indicates statistically significant difference (p-value < 0.05), * indicates statistically significant difference (p-value < 0.1), between shade and full sun temperature values within a species.

<table>
<thead>
<tr>
<th></th>
<th><em>Mahonia fremontii</em></th>
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<th><em>Pinus monophylla</em></th>
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<tbody>
<tr>
<td></td>
<td>30% shade</td>
<td>Full sun</td>
<td>30% shade</td>
<td>full sun</td>
</tr>
<tr>
<td>Pot</td>
<td>41.8 +/- 0.7**</td>
<td>49.9 +/- 1.1**</td>
<td>42.4 +/- 0.6**</td>
<td>49.3 +/- 1.2**</td>
</tr>
<tr>
<td>Leaf</td>
<td>35.1 +/- 0.5**</td>
<td>38.5 +/- 0.5**</td>
<td>35.6 +/- 0.6**</td>
<td>39.3 +/- 0.6**</td>
</tr>
<tr>
<td>Soil</td>
<td>19.5 +/- 0.4**</td>
<td>24.5 +/- 0.3**</td>
<td>21.5 +/- 0.7**</td>
<td>26.1 +/- 0.6**</td>
</tr>
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greater under shade for both aboveground and PIP on most dates throughout the season, as shown in Fig. 1. In 2010, the difference in mean conductance values between shade and full sun were less distinct. Graphically, the means still show the trend of being higher under the shade, although this effect was only highly statistically significant on one date in the aboveground study, and moderately significant on two dates in the PIP as shown in Fig. 1. Because differences in $g_s$ values between sun and shade were seen more frequently during the first year, it seems likely that shade may be more important to *M. fremontii* growth during establishment periods. During periods of stress, such as after repotting, the effect of shade on $g_s$ is more apparent. When the plants become more established, the effect of shade on $g_s$ is less evident, as shown in Fig. 1. Because increased $g_s$ can be indicative of higher photosynthesis, it may be inferred that growing plants under shade after repotting has a positive effect. In a similar shade study performed on another arid habitat shrub, *Enchylaena tomentosa*, it was found that relative growth rates were much higher for shaded seedlings during establishment periods (Hastwell and Facelli, 2003).

When dawn-to-dusk $g_s$ was measured on 12 June 2010, $g_s$ was shown to be greater under shade at many times throughout the entire day, as shown in Fig. 2. Graphically, the shaded PIP plants’ $g_s$ means appeared to be consistently about 100 mmol m$^{-2}$s$^{-1}$ greater. However, due to high variances, these differences were not statistically significant in the early morning and again in the late afternoon and evening. However, the difference in $g_s$ was significant between 10:30 AM and 3:00 PM as shown in Fig. 2. The aboveground plants’ $g_s$ showed a slightly different trend. While, graphically, the differences between shade and full sun did not seem as great as in the PIP, the differences
Figure 1. Seasonal stomatal conductance ($g_s$) for *Mahonia fremontii* comparing 30% shade versus full sun treatments grown aboveground and PIP for the years 2009 and 2010. Measurements were made using the SC-1 Decagon Leaf Porometer (Decagon Devices, Pullman, WA, USA). ** indicates statistical significant difference (p-value < 0.05), * indicates statistical significance difference (p-value < 0.1), between shade and full sun $g_s$ values.
Figure 2. Dawn-to-dusk stomatal conductance ($g_s$) for *Mahonia fremontii* comparing 30% shade versus full sun treatments grown aboveground and pot in pot. Data was collected from 7:30 AM to 8:30 PM on June 12, 2010 using the SC-1 Decagon Leaf Porometer (Decagon Devices, Pullman, WA, USA). ** indicates statistical significant difference (p-value < 0.05), * indicates statistical significance difference (p-value < 0.1), between shade and full sun $g_s$ values.
proved to be significant throughout most of the day. The only time that \( g_s \) was not statistically significant was during midday, when measured at noon and at 3:00 PM (Fig. 2). This convergence of \( g_s \) mean values between shade and full sun treatments coincided with the hottest part of the day, when even the shaded plants may have been heat stressed, causing stomatal closure and decreasing \( g_s \). Interestingly, the daily \( g_s \) measurements were always taken between noon and 1:00 PM. It is probable that the reason significantly higher \( g_s \) were not seen in the shade for the 2010 daily conductance measurements may be due to the time of day the measurements were conducted. If the measurements had been taken at other times throughout the day, such as in the morning and evening, it seems likely that higher \( g_s \) might have been recorded under shade in 2010.

The dawn-to-dusk \( g_s \) measurements allowed us to determine *M. fremontii*’s conductance pattern throughout an entire day. As expected, the highest \( g_s \) occurred early in the morning before the intense heat of the day. As the day warmed up conductance decreased as the stomates closed in response to the heat, as shown in Fig. 2. In the early evening, as the temperatures came back down, \( g_s \) started to increase. This data shows that the plants were most active in the early morning and evening when temperatures were cooler. This confirms our hypothesis that high heat does trigger stomatal closure in this species. It also helped to determine that the ideal time to perform photosynthesis and light response testing was in the morning, when the plants were most active.

Since greater stomatal activity was seen in the cooler parts of the day, it can be speculated that that is when the most active carbon gain is occurring. It can also be speculated that the greater conductance under shade is likely a result of the milder growing conditions provided, as the shade cloth did clearly help to reduce temperature
(Table 1). It was most likely these decreased temperatures that helped to decrease the triggers that lead to stomatal closure.

The light response testing for both *M. fremontii* and *P. monophylla* showed no difference in photosynthetic values between the full sun and 30% shade treatments at all light levels. Because no differences were observed between the treatments, all values for each light level were combined and averaged to create a single curve for each species, as shown in Fig. 3. It was assumed that the full sun plants would saturate at greater light levels than the shade plants, because they should be more acclimated to higher light levels than the shaded plants, e.g. it should take less light to cause maximum photosynthesis for the shade acclimated plants. Because photosynthetic values were not different between the treatments, it seems likely that no physiological changes took place at the leaf level, and that both treatments of the plants had the potential to utilize all available light. This, however, does not necessarily mean that full sun is more advantageous than 30% shade, as other factors such as temperature likely contribute to overall plant health and new growth.

Interestingly, it appears that the *P. monophylla* had a greater photosynthetic response than the *M. fremontii*, as shown in Fig. 3. While the two species were never meant to be directly compared to one another, the counterintuitive nature of the pattern is worthy of note. It was assumed that *M. fremontii* would have greater photosynthetic values than *P. monophylla*. *Mahonia fremontii* is initially a faster growing plant and grew a considerably more during the experiment, creating the expectation of witnessing greater photosynthetic response during testing.
Figure 3. The relationship between leaf photosynthetic rate (net CO$_2$ exchange) and photon flux density (Q) for *Mahonia fremontii* and *Pinus monophylla*. Full sun and 30% shade treatment values were not statistically different for both species and were, therefore, averaged together to create the light response curves for each species. Measurements were made with the Li-Cor 6400 IRGA gas exchange system (Li-Cor, Lincoln, NE, USA).
When photosynthesis was tested at ambient light levels, *P. monophylla* again appeared to have greater photosynthetic values than the *M. fremontii* (Table 2). Some of this effect may be explained by the times in which the measurements were performed. The *P. monophylla* were measured in the morning between 9:30 AM and 10:30 AM, whereas the *M. fremontii* were measured between 10:30 AM and 11:30 AM. During this time frame, a significant change in temperature had occurred, and stomatal closure may have been an issue. However, the afternoon measurements also showed that photosynthesis still appeared to be greater for the pines, even when afternoon *P. monophylla* measurements were compared to morning *M. fremontii* values. This indicates that another factor may be contributing to the pines’ greater photosynthetic values. It is possible that this may have been caused by an error in measurement, as the *P. monophylla* leaves do not completely cover the hole when enclosed in the cuvette the way most larger leaves do. Therefore, in order to take a measurement, it was necessary to estimate the surface area being measured. Although careful measurements were taken, it is possible that this area was underestimated, causing the resulting data to appear too high. If this is the case, then the actual values of the data collected for *P. monophylla* with the Licor 6400 (photosynthesis, transpiration, and conductance) would seemingly be smaller. However, even if the actual values are inaccurate, the measurements were all made with great precision and can still be used to validly compare the relative differences between shade and full sun *P. monophylla*.

The real purpose of the photosynthesis testing was not to compare the two species, but rather to compare the treatments (shade vs. full sun) at different times of the day (morning and afternoon) for each species. For both species, the greatest
Table 2. Photosynthetic rates (Photosynthesis), Transpiration, and stomatal conductance (Conductance) for *Mahonia fremontii* and *Pinus monophylla* comparing 30% shade versus full sun treatments in the morning and afternoon. Measurements were made using the Li-Cor 6400 IRGA gas exchange system (Li-Cor, Lincoln, NE, USA).

Photosynthetic rates are a measurement of the exchange of CO₂ in μmol m⁻² s⁻¹. Transpiration and conductance are measured in mmol m⁻² s⁻¹. ** indicates statistically significant difference (p-value < 0.05), * indicates statistically significant difference (p-value < 0.1), between shade and full sun photosynthesis, transpiration, and conductance values within a species.

<table>
<thead>
<tr>
<th></th>
<th>Morning</th>
<th>Afternoon</th>
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<tbody>
<tr>
<td><strong>Mahonia fremontii</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Photosynthesis</td>
<td>10.2 +/- 0.7</td>
<td>9.6 +/- 1.5</td>
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<tr>
<td></td>
<td><strong>10.0 +/- 0.4</strong></td>
<td><strong>4.7 +/- 0.7</strong></td>
</tr>
<tr>
<td>Transpiration</td>
<td>3.48 +/- 0.27</td>
<td>3.45 +/- 0.33</td>
</tr>
<tr>
<td></td>
<td><strong>4.19 +/- 0.65</strong></td>
<td><strong>3.01 +/- 0.17</strong></td>
</tr>
<tr>
<td>Conductance</td>
<td>106.5 +/- 11.5</td>
<td>101.6 +/- 10.8</td>
</tr>
<tr>
<td></td>
<td><strong>99.9 +/- 8.9</strong></td>
<td><strong>70.6 +/- 4.3</strong></td>
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| **Pinus monophylla**  |                  |                  |
| Photosynthesis       | 20.4 +/- 4.6     | 13.6 +/- 0.3     |
|                      | 12.6 +/- 2.5     | 12.7 +/- 0.4     |
| Transpiration        | 4.96 +/- 0.65    | 3.11 +/- 0.35    |
|                      | 4.41 +/- 1.18    | 5.15 +/- 0.87    |
| Conductance          | 150.5 +/- 19.4   | 114.4 +/- 12.5   |
|                      | 114.5 +/- 17.1   | 126.1 +/- 9.8    |
photosynthesis appeared to occur under shade in the morning (Table 2). This seemed especially evident with the shaded *P. monophylla*, whose average photosynthesis in the morning was a value of 20.35 \( \mu \text{mol m}^{-2} \text{s}^{-1} \), compared to 13.6 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) in full sun (Table 2). However, due to high variances in the data, the differences in all of the gas exchange data (photosynthesis, transpiration, and conductance) comparing shade and full sun *P. monophylla* proved to be not significant.

In the afternoon, the mean photosynthetic rates of both treatments for *P. monophylla* are approximately the same (Table 2). This indicates that the shade protection helps only to a certain extent, and that as daily temperature increases, the shade protection is not enough to stop stomatal closure, causing a decrease in photosynthesis. This is a very significant finding, as it offers an explanation as to why the pines did not actually grow more in the shade treatment. Although they appeared to have greater photosynthesis in the early morning, it did not last very far into the day and therefore was not enough to cause greater above-ground growth.

*Mahonia fremontii*, however, showed a much different trend. The shade and full sun treatment means for all the gas exchange data (photosynthesis, transpiration, and conductance) were much closer and not statistically significant in the morning. However, when tested again in the afternoon, photosynthesis, transpiration, and conductance were all significantly greater in the shade treatment plants (Table 2). The shaded plants had approximately the same photosynthetic rates that they had had in the morning, whereas the full sun plants had significantly dropped by the afternoon. This finding indicates that the shade was definitely beneficial for the *M. fremontii*, as mid-summer days are long and hot. It is apparent that it was during this time frame when the shade treatment was
benefitting the *M. fremontii* most, whereas there was no difference with the *P. monophylla* photosynthesis, transpiration, and conductance between shade and full sun treatments during the high temperatures of the afternoon. This continuation of higher photosynthetic activity into the afternoon for the shaded *M. fremontii* is a possible reason that greater growth was recorded for *M. fremontii*, and not for *P. monophylla*.

Moderation of high temperatures and intense sunlight using 30% shade can be linked to a significant increase in *Mahonia fremontii* growth in the aboveground plot (Table 3). However, there was no significant or even visually apparent growth difference between shade and full sun *M. fremontii* either year in the PIP experiment. There was also no significant growth difference between shade and full sun treatments for *Pinus monophylla* in both the aboveground and PIP studies.

In the aboveground *M. fremontii* study, there was one extreme outlier. One particular full sun *M. fremontii* outgrew the next highest growing subject (a shade plant) by 20 cm. This outlier subject grew 65 cm in 2010, whereas the next’s highest growing plant, a shade plant, grew 40 cm in 2010. It is hypothesized that the outlier plant may have a genetic mutation that caused increased growth rates. This plant, along with other *Mahonia* from the study, will be planted out in the spring of 2011 and continued observations will be made to determine if the plant is truly a more rapid growing specimen. If this plant continues to outperform other plants, then a more appropriate variety to grow and introduce to the nursery industry may have been discovered.

Moderation of root-zone temperature through the use of PIP did not have a positive effect on growth for either species (Table 3). In fact, both species appeared to have higher growth in the aboveground plot. This was especially obvious with the
Table 3. Average shoot elongation measurements (cm) of *Mahonia fremontii* and *Pinus monophylla* for aboveground and pot-in-pot, comparing 30% shade versus full sun for the years 2009 and 2010. ** indicates statistically significant difference (p-value < 0.05), * indicates statistically significant difference (p-value < 0.1), between shade and full sun growth within a species.

<table>
<thead>
<tr>
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<th>2009</th>
<th>2010</th>
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<tbody>
<tr>
<td></td>
<td>30% shade</td>
<td>full sun</td>
</tr>
<tr>
<td><em>Mahonia fremontii</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>above ground</td>
<td>15.7 +/- 2.1</td>
<td>8.6 +/- 2.2</td>
</tr>
<tr>
<td>pot-in-pot</td>
<td>7.9 +/- 2.3</td>
<td>10.7 +/- 3.8</td>
</tr>
<tr>
<td><em>Pinus monophylla</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td>above ground</td>
<td>3.9 +/- 0.6</td>
<td>3.9 +/- 0.6</td>
</tr>
<tr>
<td>pot-in-pot</td>
<td>4.3 +/- 0.5</td>
<td>7.4 +/- 1.8</td>
</tr>
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shaded aboveground *M. fremontii*, which grew more than all other groups for this species, including both shade and full sun treatments in the PIP. In 2009, the aboveground shade plants had only slightly greater means than the PIP subjects with the greatest growth (all full sun treatments). In 2010, the aboveground shaded plants had considerably greater average growth than all other treatments. Aboveground shaded *M. fremontii* grew an average of 7 cm more than the full sun subjects in 2009 and 11 cm more in 2010. Although the aboveground plants growth cannot realistically be compared to PIP growth, because there were no replicates (only one above ground plot and one PIP plot), the graphical data is compelling and leads to the possible conclusion that the greatest growth for *M. fremontii* can be achieved by growing them under shade and above ground.

While more growth was expected under shade conditions, greater growth was also anticipated in PIP versus aboveground. Typically, PIP allows for better root and shoot growth than that of aboveground growing systems (Schluckebier and Martin, 1997). This is a result of cooler root zone temperatures, and therefore less root stress (Ruter, 1993). The lack of increased growth in the PIP experiment may be explained by the aboveground growing system more closely resembling *M. fremontii*’s natural habitat. *Mahonia fremontii* tends to grow in highly heat conductive rocky and sandy soils (Mee, 2003). The exposed pots in the aboveground growing system are subject to more temperature fluctuation than the more stable PIP root zones. This may more closely mimic the plants’ natural environment and therefore better accommodate its physiological growth requirements.

*Pinus monophylla* exhibited no positive effect of shade on growth for both years (Table 3). In fact, it appeared that the full sun plants in the PIP plot had the greatest
growth in 2009. However, due to high variance in the growth averages this difference was not statistically significant. In 2010, the *P. monophylla* growth followed a pattern similar to that of *M. fremontii*, and graphically had greater averages in the aboveground plot. Unlike the aboveground *M. fremontii*, there was no shade effect on growth. In 2010, there was no recorded difference between *P. monophylla* growth in shade or full sun for either plot. The difference between aboveground and PIP growth, although visually compelling, cannot be statistically analyzed because, as stated previously, there was only one replicate. As with the *M. fremontii*, the reason for this greater aboveground growth, is most likely caused by the above ground growing system more closely resembling *P. monophylla*’s natural environment. In the natural environment the root zone is exposed to higher temperatures, as *P. monophylla* also grows in highly heat conductive rocky and sandy soils (Mee, 2003).

Other possible explanations may clarify why the PIP plants did not exhibit more growth than the aboveground subjects. In the aboveground plot, border plants surrounded and potentially sheltered the treatment plants, a condition not replicated with the PIP experiment. The lack of border plants in PIP may have provided greater ventilation at the leaf level and more exposure to vapor pressure deficits that could potentially result in stomatal closure. The blocks of the aboveground study (border plants and treatment plants) may have acted like small microclimates and created conditions more conducive to growth.

Most of the tests performed produced data that supports seeing greater growth for *M. fremontii* under shade for both aboveground and PIP. This is supported by the finding that both conductance and photosynthesis are greater under shade in both experiments.
However, only significantly greater growth for shaded plants in the above ground study was observed, with no significant growth difference in the PIP plants between treatments.

**SEM Images**

Although some differences in the growth rates, $g_s$, and photosynthesis between 30% shade and full sun were observed, the SEM images did not reveal any obvious physical and morphological differences between treatments for either *Mahonia fremontii* or *P. monophylla*. However, the SEM images do reveal interesting physiological adaptations that provide protection and allow these species to thrive in their semi-arid habitats.

The *Mahonia fremontii* leaves, for instance, are covered in what appears to be small waxy cuticle protrusions. Both shaded and full sun leaves appear to have the same amount and size of these cuticle protrusions (Fig. 4). These raised areas are present on both the upper and lower side of leaves, most likely to decrease wind speed across the leaf surfaces and affect the angle of sunlight upon the leaf, reducing transpiration and conserving water. *Mahonia fremontii* leaves appear to have much less protection from wind and intense sunlight than other plants growing in similar habitats, such as *Shepherdia rotundifolia* and *Eriogonum corymbosum* (Fig. 5). In comparison, these plants seemingly have much greater leaf protection, possessing not only the raised areas on the epidermis, similar to the *Mahonia fremontii* leaves, but also a large network of other protective adaptations. The *E. corymbosum* leaf surfaces are covered on both top and bottom with a large amount of pubescence. *Shepherdia rotundifolia* is covered on top with large pinwheel shaped leaf surface shields, and on bottom with large asterisk shaped shields. By comparison, the leaves of *Mahonia fremontii* appear relatively unprotected.
Figure 4. Leaf cross-sections comparing full sun leaf to 30% shade treatment leaf for *Mahonia fremontii* (images A and B). Underside leaf surfaces for *Mahonia fremontii* comparing full sun and 30% shaded leaves (Images C and D) (scanning electron micrograph).
Figure 5. Cross-section view of *Shepherdia rotundifolia* (left) and *Eriogonum corymbosum* (right) (scanning electron micrograph).
*Mahonia fremontii*’s ability to withstand frequent drought must therefore be mostly attributed to its glaucous blue leaves. *M. fremontii* has highly blue leaves, even when compared to other desert species. Glaucous leaves are very advantageous to plants that are exposed to large amounts of solar radiation. Heavily glaucous leaves are capable of reflecting large amounts of ultraviolet radiation (Mulroy, 1979). The absorption of excessive amounts of short wavelength solar radiation leads to the breakdown of cellular tissue and the near-infrared radiation can cause non-optimal and life threatening leaf temperatures. The glaucous blue leaves are most likely the adaptation that allows *M. fremontii* to thrive without the added pubescence and shielding that are seen on other semi-arid desert species.

The SEM images of *P. monophylla* also reveal some unique leaf adaptations. As a result of *P. monophylla*’s unique single-leaf characteristic the leaves are highly cylindrical, as shown in Fig. 6. Other pine species’ leaves divide into multiple leaves per fascicle as they are produced. When the closely related *P. edulis* first produces new leaves they appear to be a single leaf per fascicle and look very similar to those of *P. monophylla*, but as they develop they split right down the middle to reveal two distinct leaves per fascicle. *P. monophylla* leaves never split, maintaining their cylindrical shape. This trait decreases surface area and the number of stomata, in turn decreasing transpiration. Where the needles split they have additional flat surfaces that are covered in rows of stomata, as shown in Fig. 7. The outer convex surfaces are also covered in stomata, as shown in Fig. 8.

In all the pines analyzed, the stomata are located in long bands running the length of the leaves, so more leaves and the resulting greater surface area typically mean more
Figure 6. Leaf surface and cross-section images of *Pinus monophylla* (scanning electron micrograph).
Figure 7. Cross-section images of four pine species: *Pinus monophylla*, *Pinus edulis*, *Pinus nigra*, and *Pinus flexilis* (scanning electron micrograph).
Figure 8. Leaf surface images of four pine species: *Pinus monophylla, Pinus edulis, Pinus nigra*, and *Pinus flexilis* (scanning electron micrograph).
stomata. In Table 4, the number of stomata present per fascicle for each species have been compared, showing that the five-needled pine (*P. flexilis*) has the highest amount of stomatal bands per fascicle, whereas the single leaf of *P. monophylla* has the least. *P. flexilis* is a high elevation species that grows on the ridges of high mountains up to timberline (Earle, 2010). This habitat receives much more annual precipitation and has a much shorter growing season than that of the desert pine species. Due to its habitat, it is logical that *P. flexilis* would have the highest amount of stomatal bands, as more stomata can lend to greater conductance and more carbon gain. With the combination of a short growing season and less air due to high elevation, these trees need to maximize their potential to acquire carbon. With adequate soil moisture and the cooler temperatures of the high altitude, there is little need to transpire sparingly. This is an enormous contrast to the physiology of the desert pines, which need to carefully control transpiration.

After *P. flexilis*, *P. nigra* has the next greatest amount of stomatal bands per fascicle (Table 4). A European native, *P. nigra* is endemic to considerably more mesic and less intensely hot climates than both *P. edulis* and *P. monophylla* (Earle, 2011). As a result, *P. nigra* has more stomata, the capacity for greater photosynthesis, the potential for much greater growth rates than *P. edulis* and *P. monophylla*, and can grow more than 0.3 m per year (Van Haverbeke). This is a substantially faster growing pine than *P. edulis* and *P. monophylla*, whose growth rates are typically less than 10 cm per year.

Another significant adaptation of *P. monophylla* was revealed in the SEM images. The stomatal bands are recessed in furrows that travel the length of the leaf in *P. monophylla*. As shown in Fig. 6, these furrows appear as long white lines and are quite recessed. At higher magnification, the leaves appear to have smaller secondary furrows
Table 4. Summary of four pine species (*Pinus monophylla, P. edulis, P. nigra, and P. flexilis*) comparing the location, density, and number of stomata bands per fascicle. Data was gathered by analyzing SEM images for each species.

<table>
<thead>
<tr>
<th>Pinus species</th>
<th># of leaves per fascicle</th>
<th>Inner stomata bands</th>
<th>Outer stomata bands</th>
<th>Inner stomata density per band</th>
<th>Outer stomata density per band</th>
<th># of stomata bands per fascicle</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>monophylla</em></td>
<td>1</td>
<td>20</td>
<td>12-13/mm</td>
<td></td>
<td></td>
<td>20</td>
</tr>
<tr>
<td><em>edulis</em></td>
<td>2(3)</td>
<td>6</td>
<td>6</td>
<td>12/mm</td>
<td>11/mm</td>
<td>24</td>
</tr>
<tr>
<td><em>nigra</em></td>
<td>2</td>
<td>8-9</td>
<td>9-10</td>
<td>12/mm</td>
<td>11/mm</td>
<td>34-38</td>
</tr>
<tr>
<td><em>flexilis</em></td>
<td>5</td>
<td>3-4</td>
<td>2-3</td>
<td>12/mm</td>
<td>15/mm</td>
<td>40-55</td>
</tr>
</tbody>
</table>
that run the length of the leaf, giving it a corrugated appearance, as shown in Fig. 6D. Both the large and the smaller furrows are most likely adaptations that decrease wind speed across the leaf and aid in altering the angle of direct sunlight, resulting in a reduction of leaf temperature and transpiration. The leaves of *P. monophylla*, also appear to be waxy and of a highly glaucous blue color. All these adaptations combine to aid in the reduction of excessive leaf heating and liberal transpiration, making life in the hot, windy, and dry Great Basin desert possible.
CHAPTER 5

CONCLUSIONS

Overall, shading was only effective in producing significantly greater growth for *M. fremontii* when grown aboveground. Shade does not appear to affect growth when plants are grown PIP. Shade does not have a positive effect on *P. monophylla* growth. Since producing greater growth was the most important goal of this research, it appears that the effort in terms of time and money to grow *P. monophylla* under shade is not a viable option, and only worth it for *M. fremontii* when grown aboveground.

One of the most important findings of this study is that growing *M. fremontii* and *P. monophylla* PIP in #5 containers is no more effective than aboveground production. As discussed above, the aboveground plants appeared to grow more than the PIP plants for both species. This is important information, since creating a PIP production area is considerably more expensive, timely, and labor intensive than a standard aboveground area (Ruter. 1993). Many more plants can be produced above ground than PIP in the same sized area. It is, however, important to consider that all subjects were grown in #5 containers and PIP production is probably much more effective in the production of larger size material.

It is also important to consider that all subjects, both above ground and PIP, were taken into a cold frame during each winter during the study. PIP is very effective against winter die-back (Ruter. 1993). If no cold frame protection is available during the winter, then the benefits of PIP may far outweigh the costs. During this study, due to limited cold frame space, the border plants remained outdoors for the winter. More than half of the plants left aboveground completely died during the winters, whereas all of the PIP
plants survived. Even if PIP is not producing more growth in each growing period, it is still very important for winter protection. This provides further evidence that the size of the container in which the plant is grown is important. Larger plant material is much less likely to be moved to a cold frame or have a cold frame built around it. Consequently, the winter protection offered by PIP growing conditions is potentially very beneficial to larger material, as PIP material can simply be left in the field until it is ready to be repotted or sold.

Another significant finding of this study was that all of our subject plants put on the majority of each season’s growth in early spring, while still in the cold frame. It was already known that these plant types tend to produce most of their growth in the spring, but this growth was produced very early, before plants outside the cold frame had even started growing. The cold frame provided ideal early spring conditions with warm temperatures and high humidity that appeared to greatly benefit the test plants. Additional research to test this hypothesis is suggested. It would be very informative to evaluate these same species again with one subject group grown in a cold frame type greenhouse, such as high tunnel and another grown outdoors, as a high tunnel or hoop house could potentially lead to much greater growth, suggesting itself as the best way to grow these IMW plants. One potential method would be to use a hoop house in which the plastic can be removed when temperatures have stabilized in the spring and then possibly replaced with shade fabric for the heat of the summer. Based on everything observed during this study, this type of setup would probably lead to the greatest growth for these slow growing natives species.
Both of the trial subjects display traits that aid in the survival of their semi-arid desert habitats. And although no morphological differences were seen between the full sun and shade images for either species, more was learned about the physiological characteristics of these seldom studied plants. By analyzing the SEM images insight has been gained into how these plants are able to survive in their respective habitats. Most conventional landscape plants simply cannot live in these climates, and for this reason a continuing effort to find new and better ways to produce these locally native plants is vital. Increasing the ease of their production will ultimately lead to more availability for landscaping, and thus more climate suitable landscapes.
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