Seed Ecology of a Rare Sage, *Salvia dorrii* ssp. *mearnsii*

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Abstract: Although related taxa occur throughout the western United States, *Salvia dorrii* ssp. *mearnsii* is endemic to central Arizona. In part, its narrow distribution may be attributed to its limited fruit production, low seedling establishment, and germination requirements. Heavy herbivory pressures decreased the numbers of mature fruits in populations in two different vegetation zones and soil origins, desertscrub (limestone origin) and chaparrral (sandstone origin). The percentage of mature fruits was higher in populations from soils of limestone origin in desertscrub vegetation than from soils of sandstone origin in chaparral vegetation. Little in situ evidence of seedling establishment was observed during three field seasons. Germination experiments were conducted to test the effects of water, soil origin, light, and scarification. Greenhouse results suggest that *Salvia dorrii* ssp. *mearnsii* has few restrictions for germination. This taxon does not appear to have complex dormancy mechanisms, as it germinated readily without scarification. Germination occurred independent of soil origin except that germination did not occur at all in potting soil. Excessive water and direct light appear to inhibit germination. Maximum germination occurred at low water levels.

During the life of a plant, there are critical phases of its development that have the potential to limit its "tolerance range for a particular factor in the environment" (Gates et al. 1951). Often the first susceptible phases in a plant's life history are seed germination and seedling establishment. These are influenced by many factors, including restriction to specific soils (Thompson 1981), dependence on certain amounts of precipitation (Thompson 1981, Kadmon 1993, Bowers 1994), season (Harper 1977, Thompson 1981), temperature (Meyer et al. 1997), competition (Hallmark and Allen 1975), inhibitory compounds (Hallmark and Allen 1975), genetics (Meyer et al. 1989, Cabin 1996), and the availability of "safe sites" where seeds can readily germinate (Thompson 1981).

Germination requirements of woody members of the genus *Salvia* vary widely. Love (1989) found that cool-moist stratification for 8 weeks allowed maximum germination of *Salvia dorrii*. *S. mellifera* seeds are fire-adapted and germinate only when exposed to charcoal (Keeley 1986). Without any prior treatment, seeds of *S. vermiculata* germinate at a rate of 70 percent and remain viable for 7 years of low-temperature storage (Kay et al. 1988). Seeds of *S. reflexa* germinate better in soils with low osmotic potential (Weerakeen and Levett 1986). Some species of *Salvia* require scarification, cold stratification, or gibberellin treatment to induce germination and break dormancy (Love 1989, Young and Young 1992).

Seed characteristics and germination requirements have not been previously investigated in *Salvia dorrii* ssp. *mearnsii*. Limited numbers of mature fruits, low seedling establishment, and specific germination requirements may restrict its distribution in central Arizona. This subspecies is a long-lived, perennial shrub that displays no evidence of vegetative reproduction and very few seedlings in its natural environment (personal observation). It is distributed in disjunct patches in central Arizona along the Verde River from Perkinsville to Camp Verde (Figure 1) and grows in limestone- and sandstone-based soils in three vegetative zones: pinon-juniper, chaparral, and desert grassland. Its distribution is restricted as a result of many factors but does not appear to be strictly constrained by soil characteristics.

The U.S. Forest Service lists *Salvia dorrii* ssp. *mearnsii* as a sensitive species because of this limited distribution and threats to its survival. The rapid development of the Verde Valley potentially threatens the plant and its habitat. If not protected, *S. dorrii* ssp. *mearnsii* may not persist in nature. Specific activities that threaten this taxon are mining, land trades, and other development projects.

Several questions are addressed here: Does herbivory affect fruit production in *Salvia dorrii* ssp. *mearnsii*? Is fruit production of *S. dorrii* ssp. *mearnsii* different in plants from different soil origins? Is germination of this subspecies affected by soil origin, watering level, or light availibility? Knowledge of the germination requirements will aid in the conservation of this rare sage.

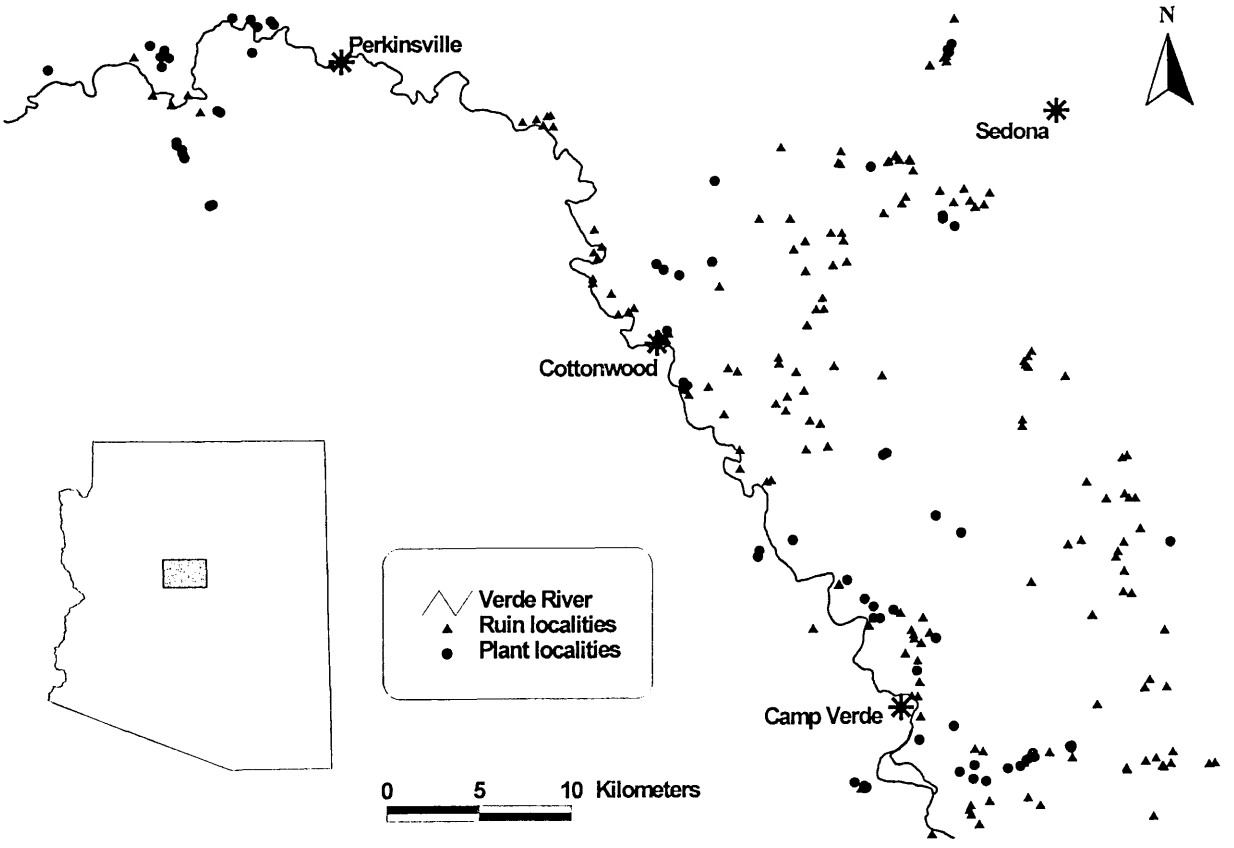

Figure 1. Distribution of *Salvia dorrii* ssp. *mearnsii* in the study area. Inset is study area on Arizona map.

Distribution and Taxonomy

Salvia dorrii ssp. *mearnsii* is one of two subspecies in the *Salvia dorrii* complex. *Salvia dorrii* ssp. *mearnsii* is geographically isolated from *S. dorrii* (Kellogg) Abrams ssp. *dorrii* (Strachan 1982). It is also morphologically distinct from *S. dorrii* ssp. *dorrii* due to its reduced stature (15–30 cm vs. 10–50 cm), narrow leaves (1.5–3 mm wide vs. 6–10 mm wide), and low number of verticels per branchlet (1–3 vs. 2–5). *Salvia dorrii* ssp. *mearnsii* is limited to central Arizona whereas the other subspecies, *S. dorrii* ssp. *dorrii*, and its varieties, var. *dorrii*, var. *clokeyi* Strachan, var. *carnosa* (Douglas ex Greene) Cronq., and var. *pilosa* (A. Gray) Strachan and Reveal, are widespread throughout the western United States and into Mexico. *Salvia pachyphylla* Epling ex Munz is closely related as well, occurring in disjunct populations in northern Arizona and Baja California. Current molecular genetics studies (Robin Taylor, unpublished data) will aid in the interpretation of the phylogenetic relationships between members of the *Salvia dorrii* complex and *S. pachyphylla*.

Geological History and Site Specificity

The Verde Valley is a northwest-trending basin that was formed by movement along the Verde fault (Cassell 1980, Nations 1981). Depositional environments in this basin led to the development of the Verde Formation, named by Jenkins (1923) because of its many limestone, sand, clay, and saline sediments.

Many of the known populations of *Salvia dorrii* ssp. *mearnsii* inhabit the eroded mesas and hills of the Verde Formation on substrates of limestone,

siltstone, and gypsum (Mahard 1949, Twenter and Metzger 1963, Cassell 1980, Nations 1981). These substrates are generally white to brown in color, hard in texture, relatively resistant to weathering, and composed of fine particles that form rough, hard conglomerations of limestone and clay. Other sedimentary substrates inhabited by *S. dorrii* ssp. *mearnsii* include iron-rich, coarse sandstones. Of the 48 known populations, 30 occur on the limestone deposits of the Camp Verde and Cottonwood regions, 4 populations inhabit the sandstone deposits near Sedona, and 14 populations occur in the Perkinsville area on interfacing soils of limestones, siltstones, and mudstones.

Plant Distribution Patterns

Although most of the Verde Valley is a depositional basin of limestones, siltstones, sandstones, basalts, and gravels, the distribution of *Salvia dorrii* ssp. *mearnsii* is limited to specific areas. At every site where the plant occurs, the population boundaries are distinct yet confounding. This subspecies is absent in adjacent areas that seem optimal. Some of the populations grow in close proximity to one another but have dramatically different soil characteristics (particle sizes, water holding capacities, and colors). The distribution of *S. dorrii* ssp. *mearnsii* cannot be completely explained by a certain chemical, physical, or biological element within these soils (Baskin and Baskin 1988).

Lacking fossil and pollen records for this subspecies, the paleodistribution of *Salvia dorrii* ssp. *mearnsii* cannot be pinpointed. According to J. Dale Nations (personal communication) and Carr (1986), there was no major structural change in the landscape of western Arizona after a drying trend (2–4 million years ago), which could have affected a continuous population of *Salvia* (Nations 1981). However, changing climatic conditions may have contributed to the isolation and evolution of *S. dorrii* ssp. *mearnsii*.

The closest relative of *Salvia dorrii* ssp. *mearnsii* is assumed to be *S. dorrii* ssp. *dorrii*. It grows in the mountains of western Arizona and California and may have extended into central Arizona in the past. Anderson (1986, 1996) noted that other basins of central Arizona similar to the Verde Valley exhibit similar floristic patterns (concentration of endemics, similar species, patchy distributions), indicating that major plant migrations have occurred across this range. Populations of plants could easily have been reproductively isolated due to climate change, causing speciation at the subspecies level (Mayr 1982, Grant 1981, Watts 1984, Price 1996).

Furthermore, palynological studies indicate that the paleoenvironment of Lake Verde consisted of many fluctuating pools of water from several inches to a few feet (Hevly 1974). This wetland environment supported reeds, rushes, cattails, and marshland algae. Surrounding this depositional basin were evergreens, low-growing shrubs, perennial herbs, and grasses (Hevly 1974). Aridland plants like *Salvia dorrii* ssp. *mearnsii* and other species similar to present-day plants inhabited the dryer slopes around Lake Verde during this time (Hevly 1974). As central Arizona slowly dried out 2–4 million years ago, this slope-upland vegetation likely colonized the lakebed deposits of the Verde basin (Dean Blinn and J. Dale Nations, personal communication) as it does today.

Materials and Methods

Herbivory and Fruit Production

To assess the impacts of floral herbivory and to ensure the collection of an adequate number of nutlets (one-seeded, indehiscent fruit) for germination experiments, inflorescences of *Salvia dorrii* ssp. *mearnsii* were wrapped with cheesecloth. When nutlets began maturing, the verticels were covered with cheesecloth and secured with twist ties. Some fruits had been damaged, so only inflorescences without evidence of herbivory were chosen. A second criterion for covering an inflorescence was the presence of at least five maturing nutlets. A total of 125 verticels were covered on plants from limestone soils and 159 were covered on plants from sandstone soils.

Mature nutlets were collected in mid June. An equal number of uncovered inflorescences were collected from the same plants for assessing herbivory. After analysis, potentially viable nutlets were stored in a refrigerator (4.5° C) for 90 days. In total, 604 viable nutlets from both covered and uncovered inflorescences were collected from plants growing in soils of limestone origin and 306 viable nutlets were collected from plants growing in soils of sandstone origin. Data from each site were pooled by soil origin, sandstone and limestone.

Chi-square tests were used to compare the numbers of mature and damaged fruits between covered and uncovered inflorescences. A mature fruit was classified as an ovary that was fertilized and swollen to some degree even if the seed inside was not fully mature and viable. An immature fruit was categorized as a fruit that collapsed

under pressure or one that had evidence of herbivory. These comparisons were conducted independently of soil type.

Soil and Fruit Production

The effects of soil origin on the floral and seed ecology of *Salvia dorrii* ssp. *mearnsii* were analyzed only for uncovered verticels. Analyzed values included the percentage of mature fruits and the percentage of fruits with evidence of herbivory (damaged). They were compared between plants from soils of different origins (sandstone and limestone) to determine if site characteristics (soil origin, elevation, temperature, precipitation) affected these variables.

Germination Experiments

Experiments were conducted to investigate how various factors affect germination in *Salvia dorrii* ssp. *mearnsii*. Greenhouse studies were conducted because it was not feasible to observe germination in the field. Soil and fruits collected from five distinct plant localities were used to test the effects of scarification, watering level, light availability, and soil origin on germination percentage.

Sample sizes were small because of the limited supply of fruits. Each treatment was allotted 36 fruits divided into 12 pots (3 inch, 250 cm^3) so that there were 3 fruits per pot (or petri dish). Closed petri dishes were used to assess the effects of scarification (eliminating other variables); the fruits were placed on wet, sterilized filter paper. All nutlets planted in soil were placed approximately 0.6 cm below the soil surface. The pots were stored in a greenhouse at 20–24° C (evening-day) and watered daily. When testing the effect of watering level, the low-water treatment pots received 10 ml of water each per day and the high-water treatment pots received 50 ml of water each per day. Fruits were placed on top of or 0.6 cm below the soil surface to test the effects of light availability, using 18 pots with 4 fruits each. When germination occurred (up to 32 days), tallies were taken. In the petri dishes, germination was determined to be successful when the cotyledons reached 0.6 cm long. Fruits that were planted in soil were considered germinated when the cotyledons appeared above the soil surface. Chi-square analyses were conducted using the total number of fruits germinated in all pots and means were used for the ANOVA comparisons. The data were not transformed.

Soil Analyses

Field moisture content and percent rock were assessed in soils of limestone and sandstone origin where *Salvia dorrii* ssp. *mearnsii* is located. Soil was collected to 8 inches deep three times throughout two field seasons. Due to the rocky nature of these soils, a shovel was used to collect the soil instead of a soil corer. Soils were weighed immediately after collection, dried for 5 days at 40.6° C, and reweighed to determine the field moisture content. The following equation was used to determine moisture for each sample: [(weight of soil before drying (g)) – (weight of soil after drying (g))/ (weight of soil before drying (g))] x 100. Percent rock was measured as athe percentage of soil weight that was occupied by particles greater than 4.75 mm. All soil was then stored at room temperature until used in germination experiments.

Results

Herbivory and Fruit Production

Herbivory negatively affected fruit production of *Salvia dorrii* ssp. *mearnsii*. Fruits from covered verticels had proportionally lower levels of herbivory (17%) than those from uncovered (64%) verticels (Chi square = 110.33, $p << 0.001$, Figure 2). The covered verticels also had a higher proportion of mature fruits (50%) than uncovered (35%) verticels (Chi square = 83.861, $p << 0.001$, Figure 3).

Soil and Fruit Production

The percentage of mature fruits was significantly different for plants from different soil origins and vegetation communities; however, herbivory was not significantly different. Plants from soils of sandstone origin in chaparral vegetation had 23 percent of fruits mature, whereas plants from soils of limestone origin in desertscrub vegetation had 43 percent of fruits mature (Chi square = 354.5, $p << 0.001$, Figure 4). Although not significantly different, the proportion of damaged fruit was 57 percent for plants from soils of limestone origin in desertscrub communities and 78 percent for plants from soils of sandstone origin in chaparral communities (Chi square = 2.537, $p > 0.05$).

Germination Experiments

Scarification did not significantly affect germination percentages of *Salvia dorrii* ssp. *mearnsii* fruits. Analyses were conducted independently of what type of soil origin in which the plants were

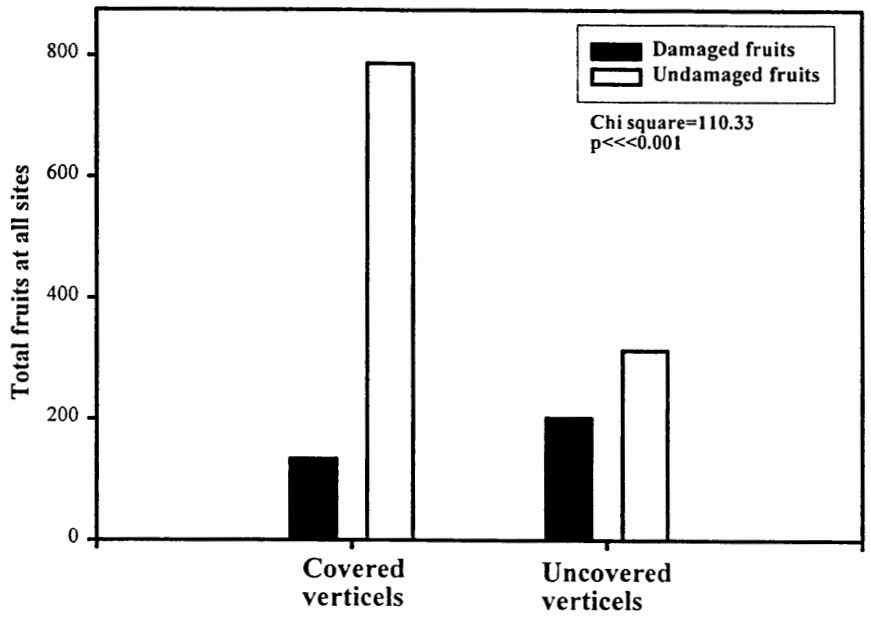

Figure 2. Herbivory negatively affects the fruits of *Salvia dorrii* ssp. *mearnsii*. Verticels that were covered with cheesecloth had significantly lower herbivory (17% of fruits damaged) than verticels that were not covered (64% of fruits damaged).

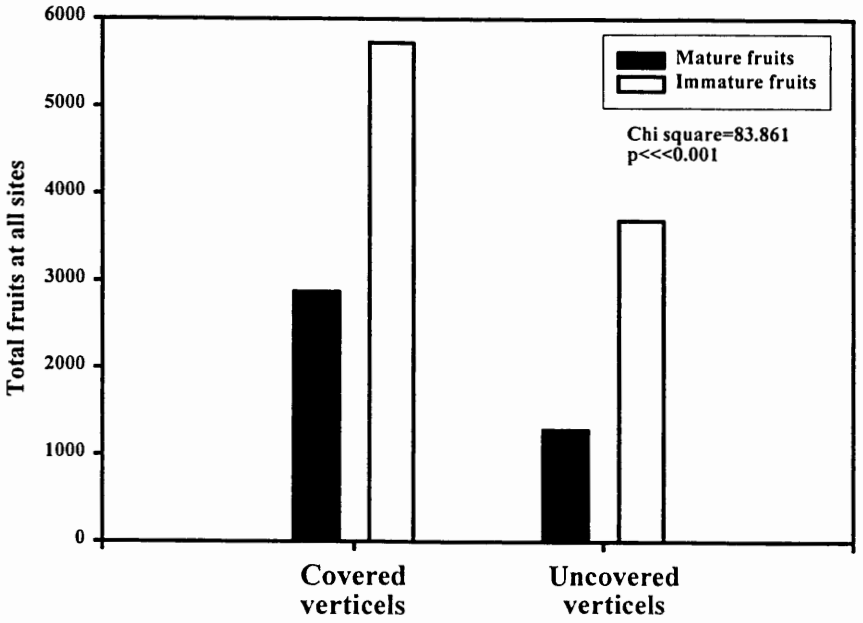

Figure 3. Fruit set in *Salvia dorrii* ssp. *mearnsii* plants was negatively affected by herbivory in all soil types. A significantly lower proportion of fruits matured in verticels that were uncovered than in those that were covered.

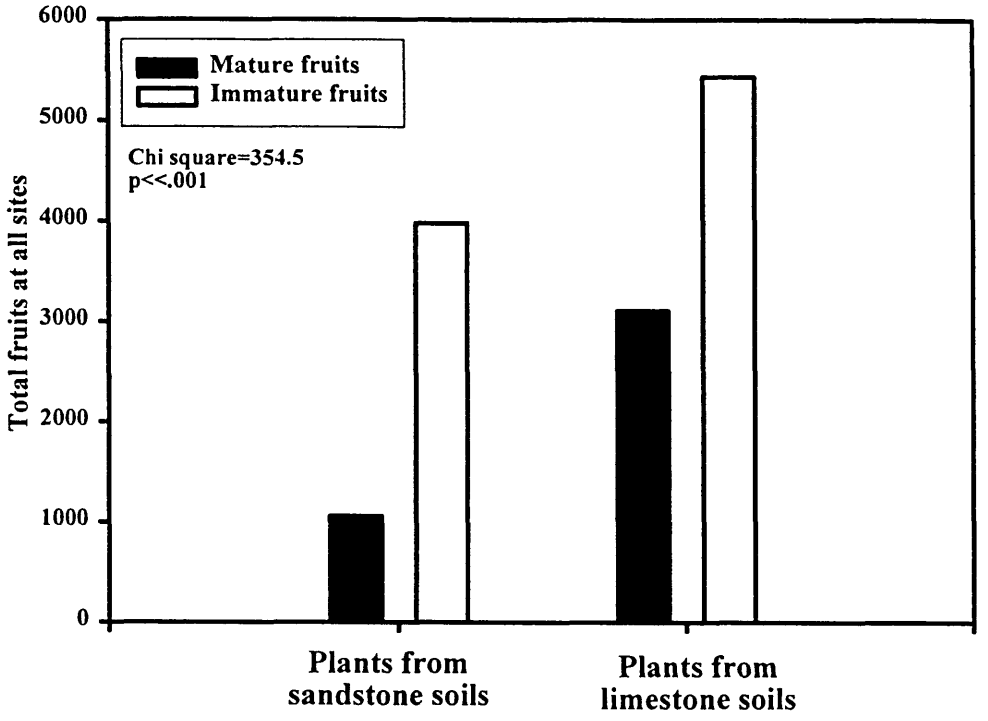

Figure 4. Fruit set varied on plants from different soil origins (limestone vs. sandstone). A significantly lower proportion of fruit was set in plants on soil of sandstone origin than plants on soil of limestone origin.

growing. Seventy-one percent of scarified fruits germinated and 66 percent of unscarified fruits germinated (Chi square = 0.1662, $p > 0.05$).

Regardless of scarification treatment, overall germination was maximized when conducted in petri dishes. Eighty-eight percent of fruits from plants in soils of sandstone origin germinated and 55 percent of fruits from plants in soils of limestone origin germinated. Chi-square analyses confirmed that these percentages were significantly different (Chi square = 12.261, $p << 0.001$).

Fruits in petri dishes had higher germination than fruits planted in soils. After 32 days, only 1 fruit of 72 from both types of soils germinated in a standard potting soil mix. When the fruits were planted in their native soils and watered heavily, fruits from sandstone soils in chaparral vegetation germinated less often (2.8%) than fruits from limestone soils in desertscrub vegetation (13.9%). Chi-square analyses indicated that planting fruits in native versus foreign soil did not affect germination percentages (Chi square = 0, $p > 0.1$). Chi-square analyses indicated that planting fruits in on-site soil versus off-site soil did not affect germination percentages (Chi square = 0, $p > 0.1$).

Soil origin and watering level significantly affected germination percentages. Fruits from plants in soils of limestone origin germinated at significantly higher percentages at low (mean = 50%) and high (mean = 22.2%) watering levels (ANOVA, Figure 5) than fruits from plants in soils of sandstone origin. Fruits from plants in soils of sandstone origin germinated similarly at low (mean = 5.6%) and high (mean = 5.6%) watering levels (ANOVA, see Figure 5).

The amount of light reaching the fruits (placement) did not significantly affect their germination. In this particular trial, soil origin was a covariate to eliminate the effect of soil in the analysis. At both watering levels, mean germination percentage was higher, although not significantly, for fruits that were placed on top of the soil surface than those that were buried 0.6 cm under the soil surface (ANOVA, $p = 0.069$, Figure 6). This experiment reiterates the results that fruits germinate more frequently at low watering levels (ANOVA, $p = 0.001$, see Figure 6), as shown above.

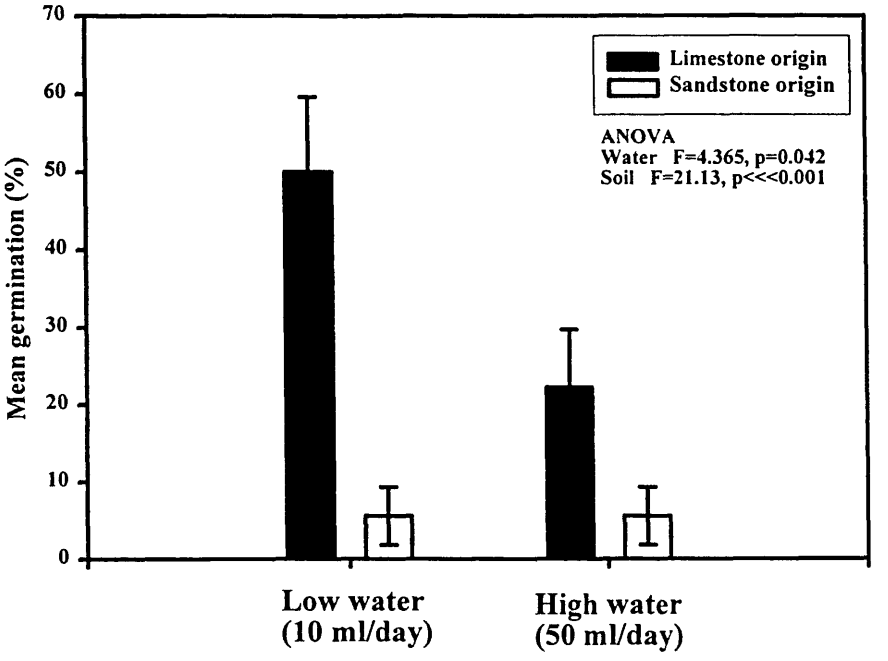

Figure 5. Germination experiments tested the effects of watering level and soil origin (seeds were germinated in different soils). Seeds from plants on soils of limestone origin had significantly higher percent germination than plants on soils of sandstone origin at both low and high watering levels. Germination percentages were similar for plants on soils of sandstone origin at both watering levels.

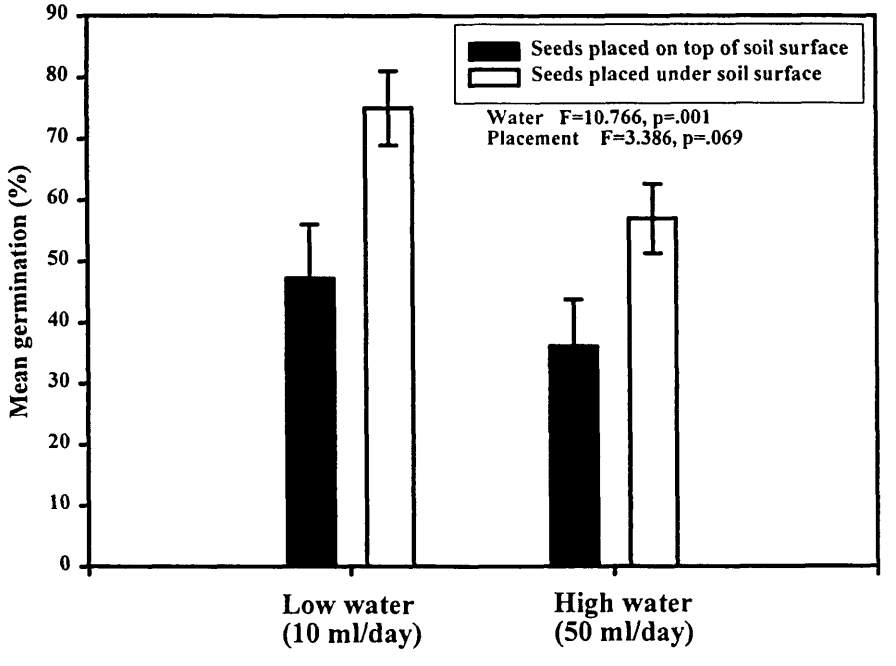

Figure 6. Germination experiments tested the effects of light availability and watering level. Soil origin (limestone vs. sandstone) was included as a covariate to eliminate its effects on germination. Note that watering level significantly affects germination although the placement of the seeds (top vs. under soil) is not a significant variable.

Soil Analyses

The percent of field water content varied for different soils of different origin. In all months of collection, soils of limestone origin (mean = 3.3%) had significantly lower field water content on average than soils of sandstone origin (mean = 11.4%; ANOVA, $F = 10.187$, $p << 0.001$). The percent of rock did not vary significantly between soils of sandstone origin (mean = 34%) and soils of limestone origin (mean = 44%; ANOVA, $F = 2.444$, $p > 0.07$).

Discussion

Herbivory and Fruit Production

Fruits of *Salvia dorrii* ssp. *mearnsii* are adversely affected by herbivory. Although other herbivores may have an effect, the most dominant herbivore observed was a caterpillar from the order Lepidoptera (Peter Price, personal communication). Exact identification could have been obtained through examination of the adult butterfly but that was beyond the scope of this study. The caterpillars were large enough that the cheesecloth covers effectively isolated them from the maturing fruits. The covers decreased herbivory pressure, which allowed more fruits to mature; however, some of the fruits were still damaged. It is likely that caterpillars were inside of these verticels when they were covered. Although uncovered verticels had the potential for additional pollination and fertilization, heavy herbivory adversely affected them. This was seen in plants from both limestone and sandstone soils, suggesting that fruit herbivory in this taxon is independent of soil and microsite characteristics.

Herbivory appears to be one cause of unviable fruits. However, some ovules (though pollinated) were unviable due to early collection; all verticels on one branchlet were collected at one time. In addition, the cheesecloth covers may have affected fruit maturation by changing the temperatures of the maturing fruits.

Soil and Fruit Production

Herbivory affects fruit production in this subspecies of *Salvia* in all environments. Overall, plants from soils of sandstone origin in chaparral vegetation had fewer mature fruits than plants from soils of limestone origin in desertscrub vegetation. The relatively dense chaparral vegetation (soil of sandstone origin) may support a greater number and variety of herbivores that feed on the aromatic fruits of *Salvia dorrii* ssp. *mearnsii*. In contrast, the sites on soils of limestone origin are more open and do not support as much nutrient-rich vegetation that is favorable to herbivores (Janzen 1974, Coley et al. 1985). Coley et al. (1985) also suggested that nutrient-poor soils, like those of limestone origin in the Verde Valley, support fewer herbivores because of limited resources in the plants on these soils. Water availability, varying greatly in soils of different origins, is also likely to affect the number and quality of fruits produced in the chaparral and desertscrub communities of central Arizona.

Germination Experiments

The timing of germination is a key element in the survival of a plant; it varies in different habitats and with different life history characteristics (Harper 1977, Silvertown 1981, Venable and Brown 1988, Meyer et al. 1989, Meyer and Kitchen 1994). Platt (1951) found that seeds of several species readily germinated on shale barrens in Virginia during the spring months but that seedling establishment was rare due to the extreme heat and dryness of the summer months. The germination of *Salvia dorrii* ssp. *mearnsii* follows similar patterns. Although fruits are mature in May or June, germination in the field does not occur until September or October. Clearly, the dry months, June and July, are too stressful for seedling establishment to occur. Even when precipitation is heavy in central Arizona, during August and September, fruits of *S. dorrii* ssp. *mearnsii* germinate relatively sparsely in their natural habitat. The drought that follows the fall rains probably limits its germination and seedling survival (Keeley 1986, Bowers 1994).

Scarification treatments did not increase germination percentages in fruits of *Salvia dorrii* ssp. *mearnsii*. Young and Young (1992) reported that many members of the genus *Salvia* require scarification or cold treatments for germination. Love (1989) found that scarification was not as effective as alternating temperatures for maximum germination in *S. dorrii* ssp. *dorrii*. However, this subspecies does not appear to depend on scarification for germination. This suggests that aridland plants may not have complex dormancy mechanisms. Meyer et al. (1989) have proposed that nondormant species have evolved in the Great Basin Desert because they do not have the risk of premature summer germination that areas of excessive summer rain have.

Interestingly, fruits from soils of sandstone origin germinated more often than fruits from

soils of limestone origin in petri dishes but less often in soil. This suggests that fruits from plants on soils of sandstone origin are extremely viable and able to germinate but that characteristics of the native soil may inhibit germination. However, these results may also be an artifact of container versus *in situ* experimentation. Low water availability in soils of sandstone origin due to rapid drainage may also limit germination. In addition, some plants such as creosote bush (*Larrea tridentata*) release inhibitory compounds that hinder germination of other seeds (Hallmark and Allen 1975). Such compounds from other plants or within the soil may limit germination, as seen in the overall low germination percentages in soils.

Excessive amounts of water appear to be inhibitory to the germination in this taxon, given that the highest levels of germination were in the pots with low-water treatments (10 ml per day). At high water levels, a high solute load, especially in soils of limestone origin, may inhibit germination. In addition, it appears that germination in *Salvia dorrii* ssp. *mearnsii* is adapted to low precipitation environments. Fruits in wet pots may have rotted. Watering regimes in these germination trials may have poorly represented the scattered, inconsistent precipitation that is characteristic of central Arizona. Furthermore, germination experiments in soils amended with perlite, vermiculite, or peat moss are likely to give different results.

Germination was strikingly similar in native, foreign, and off-site soils. If climatic and biotic conditions were favorable, *Salvia dorrii* ssp. *mearnsii* could germinate in these marginal soils and potentially expand the range of individual populations. However, under natural conditions the boundaries of this distribution are very distinct. This suggests that factors other than soil, such as competition, herbivory, and ant frugivory—evidenced in the fruits by the presence of a polysaccharide coating when imbibed with water—limit the expansion of *Salvia dorrii* ssp. *mearnsii* (Beattie 1985, Keeler 1989, Horvitz 1991).

Although *Salvia dorrii* ssp. *mearnsii* grows in high light environments, high light availability does not appear to be a requirement for germination. In fact, fruits that were placed under the soil surface germinated at higher percentages than fruits that were placed on top of the soil surface. Water availability is a more significant factor in controlling germination in *S. dorrii* ssp. *mearnsii*.

Soil Analyses

During the greenhouse germination experiments, differences were noticed in the water drainage of soils of limestone and sandstone origin. Soils of sandstone origin were completely dry in 1 day on average, whereas soils of limestone origin tended to remain moist for at least 2 days. However, these observations contradict the findings on field moisture content that showed soils of limestone origin having significantly lower percent moisture contents. This probably reflects the differences in precipitation over an elevational gradient and differences between greenhouse and field conditions. Although pots were watered every day, drying of soils, especially the fast-drying soils of sandstone origin, potentially limited germination in the greenhouse.

Conclusion

It is extremely difficult to pinpoint the factors that contribute most to the disjunct distribution of *Salvia dorrii* ssp. *mearnsii*. As Kruckeberg and Rabinowitz (1985) stated, "Organisms do not occur where they cannot, but often they do not occur where they might." This accurately describes the distribution of this subspecies. It occurs only in certain areas that are disjunct from one another and the populations are sharply defined from the surrounding vegetation. Areas where the plant occurs are not noticeably different from areas where it is absent. In addition, the soil on and off of *Salvia dorrii* ssp. *mearnsii* sites is similar and probably does not limit its occurrence. However, there are clear differences in germination of fruits from plants growing in soils of different origins. Fruits from plants in soils of limestone origin may be better adapted to the environmental conditions found in central Arizona and therefore may germinate more readily.

In addition, the polysaccharide coating on the seeds (when imbibed with water) indicates that ant dispersal may play a role in expanding populations of this subspecies (Brad Blake, personal communication, Keeler 1989). Ants are known to be important for seed dispersal in xeric environments (Keeler 1989). Although they do not disperse seeds over long distances, they do usually cache the seed in a well-fertilized area (Keeler 1989). As in some species of *Viola* and *Datura*, ant caching helps to perpetuate plant populations where seed herbivory is high (Keeler 1989).

Throughout the course of this study, many factors that may contribute to the failure or success of germination in *Salvia dorrii* ssp. *mearnsii* were elucidated. Germination percentages were highest when the fruits were watered at low levels. Under natural conditions, the water-holding capacity of the soil and adaptability of this taxon to dry environments may limit germination and seedling establishment. The plants are certainly found in higher abundance in lower elevation sites on soils of limestone origin.

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