

**The distribution of sexes across a rainfall gradient in a subdioecious southern
California chaparral shrub *Rhus ovata* S. Watson (Anacardiaceae)**

By

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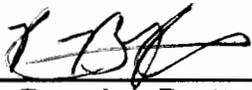
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2012

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By Heather Keldgord

**This thesis or project has been accepted on behalf of the Department of
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Abstract

Rhus ovata is an evergreen shrub species that is common to low elevations in southern California. This species is subdioecious, i.e. some individuals are functionally females and produce fruit while others are functionally male and produce flowers with pollen. *I hypothesized that because female plants allocate greater resources to reproduction through the formation of both flowers and fruit, female plants have fewer resources available for vegetative growth, survival, and defense.* Therefore, I predicted that female plants would be smaller and less competitive. I sampled *Rhus ovata* populations at six sites across a rainfall gradient (221mm/yr to 701 mm/yr) and predicted that populations would be male dominated at drier sites because of their greater stress tolerance. At each site I measured the ratio of male to female plants within the sampled population. For a subset of individuals at each site, I measured crown size, stem tissue density, specific leaf area, reproductive investment, and distance to the nearest neighbor. As expected, female plants had greater total reproductive investment although the amount of investment was highly variable and females exhibited more variability than males. However, this differential reproductive investment did not lead to sexual size dimorphism. Ratios of functional male plants to functionally female plants differed among sites, but these differences were not correlated with rainfall and across sites the ratio of males to females did not significantly differ from a one to one. Plasticity in allocation to reproduction among females in this long-lived woody species may mitigate reproductive costs and reduce sexual dimorphism.

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Introduction

Sexual Reproduction

A longstanding question in biology is why organisms have evolved sexual reproduction from asexual ancestors. On the surface, asexual reproduction appears to be a superior form of reproduction and has many advantages over sexual reproduction. For example, reproducing asexually does not require searching for a mate, which can be dangerous and costly, and asexual reproduction maximizes the number of genes an individual passes on to offspring. On the other hand, sexual reproduction provides key molecular and evolutionary advantages. One such advantage is the blending of maternal and paternal genomes, and the resultant greater genetic diversity (Thomson & Barrett, 1981; Roughgarden, 1991). Another advantage is the production of haploid gametes that aids in purging deleterious mutations that are expressed in the haploid state (Klekowski, 1988).

One cost of sexual reproduction is that it requires investment from both parents in order for offspring to survive. Each organism has a limited amount of resources that it can invest in reproduction because its access to resources is finite and it must also invest in vegetative growth, maintenance, and defense (Delph, 1990). The need to allocate resources to these competing pools gives rise to tradeoffs (Delph, 1990). According to allocation theory, an organism is under selection to balance allocation tradeoffs in a manner that maximizes fitness (Thomson & Barrett, 1981).

Most flowering plant species (94%) are hermaphrodites or are monoecious with male and female flowers on the same plant (Houston, 1979). The remaining 6%

are dioecious, where male and female flowers are found on separate individuals. The distinction between monoecious and dioecious plants is not strictly binary and there are species that contain dioecious and monoecious individuals that are called subdioecious. For subdioecious species there are two categories: first, androdioecious species have individuals that have bisexual flowers or they can have sterile female flowers and fertile male flowers (Charlesworth & Charlesworth, 1978); second, and much more common, gynodioecious species are those where individuals have either bisexual or pistillate flowers (Young, 1971). Subdioecy has been said to be a transitional state between monoecy and dioecy (Ross, 1982). In dioecious species, males and females may differ in their reproductive investment leading to divergence among the sexes. The present study examined a species that was subdioecious and fell within the gynodioecious category. Pistillate plants produce many large fruits and very little to no pollen, thereby fulfilling the functional role of female plants. On the other hand hermaphroditic plants produce prodigious amounts of flowers and very few and small fruits. Although this is not a strictly dioecious species, I use “male” and “female” throughout the remaining text to refer to hermaphrodites and pistillates respectively.

Reproductive Investment

The sexes are generally not equal in the amount and type of resources they invest in their offspring. One example is the production of the gametes and sexual structures by males and females. In general, males produce many small sperm and females produce fewer larger eggs. Except in monogamous animals, females generally have

less total offspring than males, meaning they have less chances for their genes to be passed on to the next generation, and benefit from investing more to aid the survival of each individual offspring (Andersson & Iwasa, 1996).

The chief reproductive investment for plants is the production of reproductive structures. In dioecious angiosperms, the chief investment males make is the production of the flowers and pollen (Rocheleau & Houle, 2001). This investment can be substantial, especially in wind pollinated species that must produce prodigious amounts of pollen to ensure that the pollen finds a female flower (Andersson & Iwasa, 1996). It has been found in the wind pollinated species, *Leucadendron xanthoconus*, that males have more extravagant floral displays and that this display decreases their probability of survival (Bond & Maze, 1999). More extravagant floral displays lead to increased ramification, thinner terminal branches and smaller leaves. However, in *Silene alba* females generally invest more in overall reproduction than males (Gross & Soule, 1981).

In angiosperms, females must also invest energy in developing seeds and fruit as well as flowers. The seeds often represent considerable investment in resources that provision the embryo and supply the energy needed for germination and early seedling development. These resources generally include a carbohydrate source and nutrients (nitrogen, phosphorous, potassium, and micronutrients) (Rocheleau & Houle, 2001). In closed communities, the more a female invests in her seed, the better equipped her offspring will be to survive as a seedling (Baker, 1972; Westoby et al., 1992; Moles & Westoby, 2004). Further costs for the females and males of animal pollinated species are attractants (nectar or other rewards) that

reward pollinators for visiting flowers (Anderson et al., 2006). Moreover, in virtually all angiosperm species the female is the sole provider of critical organelles, such as mitochondria and chloroplasts.

There are some factors that may mitigate parental investments. For females, flowers as well as fruit are often photosynthetic, which can partially or completely offset the carbon invested in the flower (Bazzaz & Carlson, 1979; Blanke & Lenz, 1989). Some resources invested in non-dispersed reproductive structures can be reabsorbed prior to abscission (Rocheleau & Houle, 2001). Additionally, in years where resources are scarce, long-lived plants can reduce their allocation to reproduction or eliminate it all together; this can reduce the cost of reproduction over the lifetime of the individual (Gallen et al., 1999). Because females generally invest more in reproduction than males, females may have fewer resources available for their vegetative growth, protection, and survival (Agren, 1988; Allen & Antos, 1988; Harris & Panell, 2010). Thus, females should be more limited than males to the degree they can adjust their growth and metabolism in a given environment. This limitation may lead to dimorphism between the sexes in growth or morphological differences.

Sexual Dimorphism in Dioecious Plants

Sexual dimorphism has been described for physiological as well as morphological traits in several dioecious plants species. For example the sexes may differ in plant height, ramification, leaf size, and specific leaf area (Wallace & Rundel, 1979; Dawson & Bliss, 1989; Dawson & Ehleringer, 1993; Kohorn, 1994; Kohorn, 1995;

Bond & Maze, 1999; Harris & Pannell, 2010). They can also differ in defense strategies against herbivores and diseases including the strengths of these defenses (Agren, 1987; Geber, 1995).

One of the most extensively studied dioecious species for sexual dimorphism is *Acer negundo* (boxelder). Dawson & Ehleringer (1993) showed in this species that in drier sites there are more males and wetter sites have more females. They also found that females reduced their reproductive growth and their flower and fruit production in drier areas. Males on the other hand did not reduce their reproductive growth in drier areas. Also, females were not as numerous in xeric sites because they experienced greater water stress-induced mortality. Dawson & Ehleringer (1993) also showed that the sexes demonstrated two different water stress strategies. Males closed their stomata to reduce water loss in xeric microsites and females were restricted to more mesic areas. Many aspects of boxelder sexual dimorphism are general and there are numerous other examples of ecological divergence in the sexes where females inhabit the more resource rich and less stressful sites than males (Cox, 1981; Dawson & Bliss, 1989; Queenborough et al., 2007). There is at least one example counter to this however; Jacobsen et al. (2009) found that females of a South African fynbos shrub, *Leucadendron salignum*, had stems that were more cavitation resistant than those of co-occurring males.

Co-occurring males and females of dioecious species have also been shown to occupy different microhabitats. This can be due to the differential mortality of the sexes under different environmental conditions (Bierzychudek & Eckhart, 1988). Differential mortality of the sexes is linked to greater reproductive investment for

females that leaves them with fewer resources to devote towards survival. Females can meet their greater costs by inhabiting areas that are richer in resources (Rocheleau & Houle, 2001).

Another well studied example comes from jojoba (*Simmondsia chinensis*) in arid southern California. Kohorn (1995) found that in wetter sites the two sexes of jojoba did not differ morphologically; however, in drier sites she found that males had smaller leaves and shorter internodes. Females in drier sites were driven to produce larger seeds, requiring more resources that reduced vegetative growth and lead to sexual dimorphism. The advantage of larger seeds would lead to greater tolerance of resource scarcity for offspring, which would be especially important at the critical seedling stage of development and would lead to greater offspring survival (Baker, 1972). The details of this dimorphism were further elucidated by Wallace & Rundel (1979) who showed that males had more closed canopies with a lot of self shading of leaves whereas females had more open canopies with little self shading. They also found that leaves were a greater proportion of vegetative growth in females than in males and that this proportion increased with the size of the seed set. This allowed females to reduce vegetative growth without reducing photosynthetic area.

Beyond visible morphological dimorphism, sexes of dioecious plants can also differ in their physiological attributes. For example, in *Leucadendron* spp. (Proteaceae), females have fewer branches that are larger in size with larger leaves (surface area) (Gross & Soule, 1981). A physiological cause for this could be that thicker branches allow for better hydraulic conductivity (Jacobsen et al., 2007). Furthermore, females in *L. salignum* were found to have greater xylem water stress

resistance (estimated as cavitation resistance) (Jacobsen et al., 2009).

Physiological divergence is also found in *S. chinensis*. Wallace & Rundel (1979) have shown that females have greater water storage capacity than males because their leaves are larger, heavier, and have greater water holding capacity. Since females produce fruit during the hot and dry season they have a greater need for water storage ability than males. A similar example was found by Correia & Barradas (2000) in *Pistacia lentiscus*. In this species males were found to dominate less disturbed, older areas where there was greater competition for water uptake and they were more able to tolerate summer conditions. This was most likely due to reduced investment in the root system by females.

Sexual selection and pollinator selection may also drive sexual dimorphism and a particularly well studied example comes from the genus *Leucadendron*. In wind pollinated *Leucadendron* species, males are more branched than females presumably because sexual selection pushes males to increase their number of inflorescences thereby increasing their pollen output (Harris & Pannell, 2010). In the insect pollinated species, *L. xanthoconus*, Hemborg & Bond (2005) found that differing floral rewards seems to be the working mechanism for sexual dimorphism. The greater branching in males leads to a larger showier inflorescence display that increases pollinator visitation. Pollinators visit male flowers to receive food in the form of pollen, as well as mating and egg laying sites. On the other hand, pollinators visit female flowers, which lack nectar, but are cup shaped and offer protection from the rain.

Dimorphism in Subdioecious Species

Subdioecious species have been far less studied than dioecious species with respect to sexual dimorphism. The few studies that have been conducted have found evidence that, like dioecious species, subdioecious species exhibit sexual dimorphism. In *Honckenya peploides* (Caryophyllaceae), a dune plant native to the Mediterranean Basin, Vilas & Retuerto (2009) found that fruiting females had less underground biomass (i.e.: roots), thereby decreasing their ability to acquire below ground resources. Due to the greater investment in above ground biomass for reproduction, females invested less in underground biomass and were unable to tolerate the more stressful microhabitats. Males on the other hand were able to meet their resource needs in the harsher microsites that had greater salinity and exposure, and lower nutrients and water. In another subdioecious species, *Hebe subaplina* (Scrophulariaceae), females produced more fruit and larger fruits than males. Overall females invested 4.7 times more biomass than males to fruit and two times more biomass to fruit and flowers together than males invest in pollen (Delph, 1990).

A Californian case-study

The Mediterranean-type climate regions (MTCR) across the globe are dominated by evergreen shrub species with thick leathery leaves, many of which are dioecious (Table 1). In the Cape Region of South Africa, dioecious species make up about 18% of the species in the fynbos vegetation type (Steiner, 1988). In the Spanish Mediterranean dioecy is present in 27% of the species (Herrera, 1987) and 9% in

the Chilean MTCR (Arroyo et al., 1993). Dioecy is extremely rare in the MTCR in southwestern Australia (Bell, 1991). The California MTCR region, which is dominated by a vegetation type called the chaparral, contains a wide variety of perennial shrubs, about 3% of which are dioecious (Freeman et al., 1980).

Little is known about subdioecious species in chaparral. I examined sexual dimorphism and the distribution of males and females the evergreen subdioecious chaparral shrub *Rhus ovata* S. Watson (Anacardiaceae). *Rhus ovata* has a relatively narrow distribution and occurs in southern California and a few regions in Arizona and Baja California. It spans a broad rainfall gradient in southern California from about 889 mm/yr in the wettest areas (San Bernardino and Los Angeles counties) to about 114 mm/yr in the driest areas in the Mojave and Sonoran Deserts (Hanes, 1971). This large range allows ample opportunity for habitat segregation to occur between the two sexes.

In *Rhus ovata*, females produce large amounts of fruit in addition to flowers, while males only produce flowers. Since female plants allocate a greater amount of their resources to their individual offspring via fruit production, I predicted they would have fewer resources available for vegetative growth, survival, and defense. Additionally, if there is an energy cost associated with developing greater levels of stress resistance or tolerance then females may be less able to develop the necessary high levels of stress tolerance. Therefore, I predicted that they would be less abundant in areas where resources are limiting.

A key limiting resource in semi-arid southern California is water. Mediterranean-type climate regions are defined by having cool wet winters and hot

dry summers. Plants in these regions are exposed to severe water stress during the protracted summer dry period. I predicted that, across a rainfall gradient, females would be found at equal or greater ratios to hermaphrodites in wetter sites and males will be more abundant than pistillates in the drier sites. To test this I examined sex ratios of *R. ovata* at various sites throughout their distribution in the California chaparral. I also classified the microsites inhabited by both sexes to see if there was a significant distribution pattern. This is important because an alternative hypothesis to shifting ratios of the sexes within a rainfall gradient is that they may undergo niche segregation within a site with females occupying more mesic microsites within a site.

I also predicted sexual dimorphism in *R. ovata* since females were expected have a greater parental investment in their offspring. This greater maternal investment may lead to tradeoffs in other aspects of the females' morphology such as reduced vegetative growth. To test this I measured key physical attributes of the sexes to see if males and females differed significantly. The traits I measured included plant size, specific leaf area, stem tissue density, and flower and fruit production (total reproductive investment). I predicted that there would be less resources allocated to vegetative growth and more allocated to reproductive growth in females, and that this pattern would be reversed in hermaphrodites. Furthermore, I predicted that females would have reduced stem density and specific leaf area compared to males because these traits are associated with stressful conditions.

Methods

Site Selection

Six field sites in southern California were selected based on the amount of rainfall that they received in order to ensure a broad rainfall gradient (Figure 1). For each site, meteorological data came from Remote Automated Weather Stations (<http://www.raws.dri.edu/wraws/akF.html>). These data revealed San Jacinto to be driest site with the lowest amount of rainfall and the highest maximum temperature and Angeles to be the wettest with the highest amount of rainfall and lowest maximum temperature (Table 2).

However, the field sites also differed in many other characteristics including age since last burn, elevation, and soil profile and type. The time since last burn of the six sites studied varied greatly, with the Sherwood site containing the youngest plants and San Jacinto the oldest (Table 3). The sites selected also had a great range in elevation (Table 3), the highest being San Jacinto and the lowest being Cold Creek. General soil texture and profile was determined using the USDA Natural Resources Conservation Service Web Soil Survey (<http://websoilsurvey.nrcs.usda.gov>) (Table 5).

Determination of Plant Sex

Plant sex was determined by examining the flowers of each plant underneath an eye loop (Figure 2). A plant was considered female if it had a pistil and either a reduced or absent stamen and prodigious amounts of fruit. A plant was considered male if it

had a stamen with pollen present on the anthers, a reduced or absent pistil, and very little to no fruit.

Reproductive Investment

To determine the total reproductive investment (TRI) between the sexes, reproductive biomass was measured on 20 males and 13 females at the Angeles field site. Biomass was collected over a month long period with male biomass collected at the beginning of the sampling period to ensure collection at the height of pollen production. Female biomass was not collected until fruits reached maturity. To estimate TRI, 10 flower bunches were randomly cut from each male plant (before pollen dispersal) and female plant. These samples were dried (Model 27 Thelco drying oven, Thelco Precision Scientific, Englewood, CO, USA) at least 72 hours at 65°C and weighed (CP124S balance, Sartorius Group, Goettingen, Germany) to determine flower mass. The total number of flowers per plant was estimated by counting the number of flowers on a representative branch and counting the number of branches on a representative plant. Seed and fruit mass per plant were determined for females and scaled to the whole plant in the same fashion as flower mass. Plant size was measured by taking the basal circumference, plant height, crown diameter, and number of stems. Because larger plants may produce more flowers and fruit, measurements were standardized by plant size. Total reproductive investment (TRI) was calculated as

TRI = dry mass of flowers / basal area (for males)

TRI = (dry mass of flowers + fruit) / basal area (for females)

Sex Ratios and Sexual Dimorphism

To determine if the sex ratios of sexes changed across the rainfall gradient, the numbers of males and females were recorded at each field site (Table 3). This was done using all the plants in a defined area. This method entailed sampling a total of 60 plants and then measuring the area in which they occur.

Other traits were also measured, including plant size, specific leaf area, and stem tissue density. Plant size was measured as the height of the first 20 males and 20 females sampled at each site (except at the Sherwood site where 14 females and 12 males were sampled). Height for tall shrubs was determined by measuring as high as possible with a meter stick and then estimating the remaining height. Crown volume was calculated using plant height, crown area, and basal area.

Specific leaf area and stem tissue density (both traits that are correlated to growth rate, specific leaf area positively and stem tissue density inversely) of the 20 males and 20 females were also measured. Stem tissue density was measured as the dry mass per fresh volume of mature stems (Niklas, 1993). Stems that were roughly 10 mm in diameter were collected, cut to 4 cm in length, and dried (Model 27 Thelco drying oven, Thelco Precision Scientific, Englewood, CO, USA (1 hour at 80°C and then at least 72 hours at 65°C). The stems, including pith and bark, were then vacuumed (1/6 HP 115V 60 Hz General Electric compressor vacuum pump, General Electric Company, Fairfield, CT, USA) underwater to removed gas and

submerged into a beaker of water and weighed (CP124S, Sartorius Group, Goettingen, Germany) to determine the mass of water displaced. The mass of the water displaced was then converted into volume displaced using the density of water corrected for temperature (572 Fluke IR Thermometer, Everett, WA, USA). Specific leaf area was calculated by the surface area of the leaf divided by its dried weight. From each plant three leaves, all facing the same direction, were collected from different branches. Leaves were selected from non-shaded portions of the plant when possible. If the entire plant was shaded then leaves were chosen from an open section of the plant. Leaf area was then measured using a leaf area meter (LI-3100 leaf area meter, Li-Cor Corporation, Lincoln, NB, USA). The leaves were then dried (Model 27, Thelco Precision Scientific, Englewood, CO, USA) at least 72 hours at 65°C and weighed (CP124S balance, Sartorius Group, Goettingen, Germany).

Three attributes of the microsite of each individual were surveyed to see if the sexes were associated with specific site characteristics. These characters included rockiness of the soil on a scale of 1-4 with 1:0-10% rocks, 2:10-50%, 3:50-90%, and 4:90-100%. As an estimate of competition, the nearest neighbor was identified (Baldwin et al., 2012) and the distance from the center of its basal area to the center of the basal area of each *Rhus ovata* was recorded.

Reproductive investment between males and females was compared via a Mann-Whitney test (Minitab 16, Minitab Incorporated, State College, PA, USA) due to the different variances between the sexes. The ratio of males and females observed at each site were compared using a chi-square test. Height, soil rockiness, distance to nearest neighbor, specific leaf area, and stem tissue density were

analyzed using a general linear model ANOVA with a binary response and the sex as the dependent categorical variable (JMP 10, SAS Institute Incorporated, Cary, NC, USA).

The San Dimas appeared more disturbed than the other field sites and this most likely lead to greater distances to nearest neighbors which in turn likely lead to greater resource availability to the individuals at that site due to the reduced level of competition. Because of this, statistical analyses for stem tissue density, height, specific leaf area, crown volume, soil rockiness, and distance to nearest neighbor were also run without the San Dimas site and results were reported with and without the San Dimas site in the model.

Results

Site characteristics

When nearest neighbors were identified, I found that species composition was similar across the sites (Table 5). Furthermore, while the sites varied in their soil types, they all contained similar components such as sandy loam, gravelly loam, gravelly sandy loam, and unweathered bedrock (Table 6).

Reproductive Investment

Total reproductive investment (measured as the dry weight of flowers in males and flowers plus fruit in females, and then scaled to plant size) was greater in females than in males ($W=223.0$, $P=0.04$). Females were also found to be more variable in their reproductive investment than males (Figure 3, $F= 0.01$, $df=12,19$ $P<0.001$).

Sex Ratios and Densities

Ratios of males to females differed among sites (Figure 4). Differences in ratios were not correlated with rainfall and males and females did not significantly differ from a one to one ratio ($\chi^2 > 3.84$, $P = 0.05$) at any site except the Angeles site ($\chi^2 = 5.4$, $P = 0.03$) where males outnumbered females. Across all sites the total number of males and females also did not differ significantly from a one to one ratio. The density of the sexes (Table 6) also did not significantly differ at each site ($T = 0.57$, $df = 8$, $P = 0.59$) or across all sites ($\chi^2 = 0.002$, $P \gg 0.05$).

Sexual Dimorphism

I found that plant size (height and crown volume) and vegetative traits (specific leaf area and stem tissue density) differed across sites; however, I did not find sexual dimorphism in any of the characters I analyzed. Instead I found that the two sexes were responding similarly across the rainfall gradient and that site was the only significant factor (Figures 5 & 6; $\chi^2 = 11.62$, $df = 5$, $P = 0.04$).

Height (Figure 5A) and specific leaf area (Figure 5D) were greatest at the Cold Creek site which had an intermediate amount of rainfall. The unusually high specific leaf area of plants at the Cold Creek site may have been due to shading from other individuals as suggested by the low distance to nearest neighbor. Crown volume (Figure 5B) was also greatest at the sites that received an intermediate amount of rainfall (San Dimas, Sherwood, and Cold Creek). In contrast, stem tissue density (Figure 5C) was greatest at the driest sites (Cleveland and San Jacinto) and was lower at wetter sites.

The sites also differed in the amount of rockiness (Figure 6A) and the distance to nearest neighbors (Figure 6B). Soil was rockiest at the sites that received an intermediate amount of rainfall (Sherwood, Cold Creek, and San Dimas) and distance to nearest neighbor was lowest at the Cold Creek site. However, the sexes did not differ significantly in these microsite characteristics. Soil rockiness and distance to nearest neighbor were not different between males and females.

When sexual dimorphism was analyzed without the San Dimas site I found that males and females were significantly different in their stem tissue density ($X^2=5.23$, $df=1$, $P=0.02$) with males having a greater stem tissue density than females across all sites.

Discussion

Female plants of *Rhus ovata* were found to have a greater total reproductive investment than males and the total reproductive investment in females was more variable compared to males. The variability among females occurs because some females produced very few flowers and fruit, whereas others produced much more. It is possible that females have greater plasticity in their reproductive investment than males in response to the external environment or internal factors (Lloyd et al., 1980). This plasticity may lower lifetime reproductive investment in females and may lead to less reproductive costs than would otherwise occur. Furthermore, delaying reproduction until resources are high may increase the fitness of females for that season as well as increase the probability of females surviving to the next year during seasons when resources are scarce. By contrast, males may invest

similarly in reproduction from year to year. The years that this study was conducted (2009-2011) the average rainfall was greater than the average annual rainfall at the San Jacinto, Cleveland, and Sherwood sites as well as the San Dimas site during the 2009-2010 year (Table 2). However, the average annual rainfall for 2009-2011 was less than the average annual rainfall at the Cold Creek and Angeles sites as well as the 2010-2011 year at the San Dimas site.

Plants have a limited amount of resources that they can devote to their many needs: reproduction, survival, and defense (Hemborg & Bond, 2005). The differential reproductive investment by males and females should lead to differences in tradeoffs in the other areas by the sexes. This difference in tradeoffs can lead to physical and physiological sexual dimorphism in vegetative growth (height and crown volume), competitive ability (distance to nearest neighbor), and stress tolerance, especially drought (stem tissue density, specific leaf area). Contrary to this hypothesis, height, crown volume, leaf structural traits, nor the density of stems were different between males and females. I did not find a tradeoff in the vegetative, physiological, and ecological traits I examined in this subdioecious species.

It is possible that the greater reproductive investment by females is accounted for in ways not investigated here such as inhabiting microsites with soils higher in resources, decreasing ramification, decreased branch thickness, or shorter lifespan (Bond & Midgley, 1988; Geber, 1995; Hutline et al., 2007). Furthermore, as previously discussed, females may modulate their reproductive investment from year to year, especially in a long-lived plant such as *Rhus ovata*. This could lead to equal lifetime reproductive investment of males and females and account for the similarity I

found in height, crown volume, stem tissue density, and specific leaf area. This could also account for the occupation of similar microsites and community positions by both males and females, including no differences in distance to nearest neighbor and soil rockiness.

I found differences in vegetative traits between the sexes across sites and the sexes responded similarly across the rainfall gradient. Stem tissue density was greatest at the driest sites. This is consistent with the general trend that plants make more dense tissues in habitats with where they undergo water stress (Shumway et al., 1993; Mencuccini & Grace, 1995; Hacke et al., 2001; Jacobsen et al., 2009). The chaparral shrubland community occurs in a Mediterranean climate region with cool wet winters and hot dry summers, thereby exposing plants to water stress (Bhaskar et al., 2007). Specific leaf area was also found to be greatest at the site with the smallest distance to nearest neighbor. Greater specific leaf areas are often associated with more mesic conditions and shading. Increased water availability in mesic areas allows for greater allocation to vegetative growth and increased specific leaf area. Shading also leads to greater specific leaf area due to the lower amount of sunlight available to the plant and shading increases with a decreased distance to nearest neighbor.

When the San Dimas site was excluded from statistical analyses I found a difference among sexes in stem tissue density. Females had a significantly lower stem tissue density than males which was expected since stem tissue density is associated with stress tolerance (Jacobsen et al., 2007). Since males put fewer

resources into reproduction they may be able to allocate more resources to this trait which associated with increased stress tolerance.

Plants have limited resources available to allocate to reproduction, growth, survival, and defense. I found that in *R. ovata* greater reproductive investment in females lead to decreased stem tissue density. However, no tradeoffs were observed from increased reproduction to vegetative growth (height and crown volume), competition (distance to nearest neighbor), physiological characters (specific leaf area), or ecological characters (soil rockiness). The reason for this could be that the greater reproductive investment by females is mitigated by the reduction or elimination of reproduction when resources are scarce. Furthermore, the tradeoffs could be expressed by increased susceptibility to herbivores and pathogens, reduced ramification and leaf size, and by inhabiting soils with higher nutrient concentrations or other traits that weren't measured. More research is needed to elucidate the cost of increased female TRI on the morphology and physiology of *R. ovata*.

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Figure Captions

Figure 1. Map of the six field sites.

Figure 2. Photos of female (A & B) and male (C & D) flowers in *Rhus ovata*.

Figure 3. Mean total reproductive investment (TRI) \pm one standard error for males (n=20) and females (n=13). Females have a greater TRI than males and are also more variable. Maximum and minimum TRI for each sex are listed to the right of each mean and one standard error.

Figure 4. Sex ratio across all six sites. All but one site (indicated by *) had sex ratios that did not differ significantly from 1:1 ($\chi^2 > 3.84$). The sites are arranged from lowest to highest rainfall (in parentheses next to the site name) from left to right (n=60 for all sites except Sherwood where n=26). SJ: San Jacinto, CL: Cleveland, SH: Sherwood, CC: Cold Creek, SD: San Dimas, AN: Angeles.

Figure 5. Means \pm one standard error of four physical traits of *Rhus ovata* males (represented by circles) and females (represented by squares) at the six study sites: height (A, n \geq 26), crown volume (B, n \geq 26), stem tissue density (C, n \geq 12), and specific leaf area (SLA) (D, n \geq 12). Crown volume was calculated using basal area, crown area, and height. Different letters indicate significant differences. Sites are

represented by closed symbols and means are represented by open symbols. See Figure 2 for site abbreviations.

Figure 6. Means \pm one standard error of two microsite traits of *Rhus ovata* males (represented by circles) and females (represented by squares) at the six study sites: soil rockiness (A, $n \geq 26$) and distance to nearest neighbor (B, $n \geq 26$). Soil rockiness was determined on a scale of 1-4 with 1:0-10% rocks, 2:10-50%, 3:50-90%, and 4:90-100%. Different letters indicate significant differences. Sites are represented by closed symbols and means are represented by open symbols. See Figure 2 for site abbreviations.

Table 1. Families in the five Mediterranean-type climate regions with many or important dioecious species.

California	Australia	South Africa	Chile	Mediterranean
Aceraceae	Allocasuarina	Garryaceae	Anacardiaceae	Anacardiaceae
Anacardiaceae	Colchicaceae	Leucadendron	Rosaceae	Liliaceae
Asteraceae	Solanum	Simmondsiaceae	Valerianaceae	Rhamnaceae
Chenopodiaceae				Rosaceae
Garryaceae				Santalaceae
Salicaceae				
Simmondsiaceae				

Table 2. Meteorological data for the six field sites studied. For each site values were averaged over all years that data were available (minimum of 4 years).

Site	Average Annual Rainfall (mm/yr)	2009-10 Winter Rainfall (mm/yr)	2010-11 Winter Rainfall (mm/yr)	Average Annual Temp. (°C)	*Average Annual Minimum Temp. (°C)	**Average Annual Maximum Temp. (°C)
San Jacinto	221	372	404	17.02	1.26	35.18
Cleveland	304	405	589	17.70	6.50	34.96
Sherwood	341	404	391	17.77	8.67	34.13
Cold Creek	528	439	405	17.76	9.17	30.75
San Dimas	689	820	583	16.26	5.86	31.78
Angeles	701	632	652	15.20	4.55	30.35

- Average annual minimum temperature was calculated using the month of each year with the lowest daily average.

** Average annual maximum temperature was calculated using the month of each year with the highest daily average. (Remote Automated Weather Station, <http://www.raws.dri.edu/wraws/akF.html>).

Table 3. Field sites used and three characteristics of each site.

Site	Aspect	Age of Stand (years since last burned)	Elevation (m)
San Jacinto	Flat	*	1237
Cleveland	NE	20 **	926
Sherwood	W	6 ***	503
Cold Creek	E/W	18	480
San Dimas	SE	9	835
Angeles	N	30	1219

- This site is a Juniper woodland that has limited fuel to carry fire, thus fire is rare in that system. There are very large *Rhus ovata* suggesting that it has not burned in a long time.

** This is based off the size of the plants at this site because no fire data were available.

***This site was composed of areas that burned at two different times, one 6 years ago and another at least 20 years ago based on plant size.

Table 4. Nearest neighbor species at the six field sites, listed in descending frequency.

San Jacinto	Cleveland	Sherwood
<i>Juniperus spp.</i>	<i>Cercocarpus betuloides</i>	<i>Cercocarpus betuloides</i>
<i>Bernardia miricifolia</i>	<i>Heteromeles arbutifolia</i>	<i>Quercus berberidifolia</i>
<i>Pinus monophylla</i>	<i>Rhamnus ilicifolia</i>	<i>Rhus ovata</i>
<i>Quercus cornelius-mulleri</i>	<i>Rhus ovata</i>	<i>Malosma laurina</i>
<i>Yucca schidigera</i>	<i>Ceanothus crassifolius</i>	<i>Adenostoma fasciculatum</i>
<i>Nolina parryi</i>	<i>Quercus berberidifolia</i>	<i>Heteromeles arbutifolia</i>
<i>Agave deserti</i>	<i>Quercus palmeri</i>	<i>Malacothamnus fasciculatus</i>
<i>Gutierrezia microcephala</i>	<i>Adenostoma fasciculatum</i>	<i>Rhamnus ilicifolia</i>
<i>Rhus ovata</i>	<i>Salvia mellifera</i>	

Cold Creek	San Dimas	Angeles
<i>Ceanothus spinosus</i>	<i>Rhus ovata</i>	<i>Eriogonum fasciculatum</i>
<i>Prunus ilicifolia</i>	<i>Ceanothus crassifolius</i>	<i>Rhus ovata</i>
<i>Rhus ovata</i>	<i>Heteromeles arbutifolia</i>	<i>Eriodictyon crassifolium</i>
<i>Adenostoma fasciculatum</i>	<i>Salvia mellifera</i>	<i>Adenostoma fasciculatum</i>
	<i>Malosma laurina</i>	<i>Ceanothus crassifolius</i>
	<i>Quercus berberidifolia</i>	<i>Arctostaphylos glandulosa</i>
	<i>Rhamnus ilicifolia</i>	<i>Arctostaphylos glauca</i>
	<i>Quercus durata var. gabrielensis</i>	<i>Heteromeles arbutifolia</i>
	<i>Adenostoma fasciculatum</i>	<i>Sambucus mexicana</i>
	<i>Ceanothus oliganthus</i>	<i>Quercus berberidifolia</i>

Table 5. Soil types and soil profiles for the six field sites. (USDA Natural Resources Conservation Service Web Soil Survey, <http://websoilsurvey.nrcs.usda.gov/app/WebSoilSurvey.aspx>)

Site	Soil Type	Soil Profile
San Jacinto	Omstott-Rock Outcrop	Omstott: Gravelly fine sandy loam 0-25 cm, Weathered bedrock 25-36 cm Rock Outcrop: Unweathered bedrock 0-153 cm
Cleveland	Las Posas Gravelly Loam	Gravelly loam 0-23 cm, Clay 23-69 cm, Weathered bedrock 69-79 cm
Sherwood	Cotharin-Talepop	Cotharin: Slightly decomposed plant material 0-3 cm, Loam 3-28 cm, Weathered bedrock 28-53 cm Talepop: Gravelly Loam 0-13 cm, Weathered bedrock 13-38 cm
Cold Creek	Zumaridge-Kawenga	Zumaridge: Slightly decomposed plant material 0-5 cm, Loam 5-25 cm, Weathered bedrock 25-33 cm, Unweathered bedrock 33-58 cm Kawenga: Slightly decomposed plant material 0-5 cm, Gravelly loam 5-69 cm, Clay loam 69-94cm, Gravelly loam 94-140 cm, Weathered bedrock 140-165 cm
San Dimas	Trigo, Granitic substratum-Exchequer families-Rock outcrop	Trigo family-Granitic substratum: Loam 0-8 cm, Gravelly sandy loam 8-43 cm, Weathered bedrock 43-53 cm Exchequer: Sandy loam 0-20 cm, Unweathered bedrock 20-31 cm Rock outcrop: Unweathered bedrock 0-10 cm
Angeles	Caperton-Trigo, Granitic substratum-Lodo families	Caperton: Gravelly loam 0-43 cm, Weathered bedrock 43-53 cm Trigo family-Granitic substratum: Loam 0-8 cm, Gravelly sandy loam 8-43 cm, Weathered bedrock 43-53 cm Lodo family: Gravelly loam 0-43 cm, Unweathered bedrock 43-53 cm

Table 6. Density of the sexes at the six field sites (n=60 for all sites except San Dimas where n=26)

Site	Male (individuals/km²)	Female (individuals/km²)	Total (individuals/km²)
San Jacinto (221)	3.00E+02	4.50E+02	7.50E+02
Cleveland (304)	3.80E+03	3.33E+03	7.13E+03
Sherwood (341)	2.39E+02	2.79E+02	5.18E+02
Cold Creek (528)	9.64E+03	6.89E+03	1.65E+04
San Dimas (689)	3.36E+02	4.40E+02	7.77E+02
Angeles (701)	1.14E+04	6.16E+03	1.76E+04

Figure 1

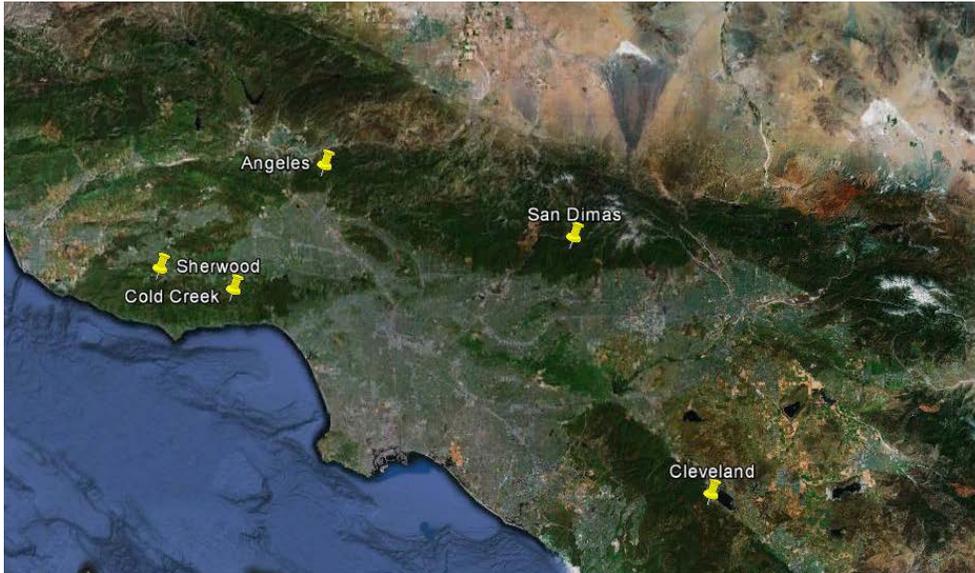


Figure 2



Figure 3

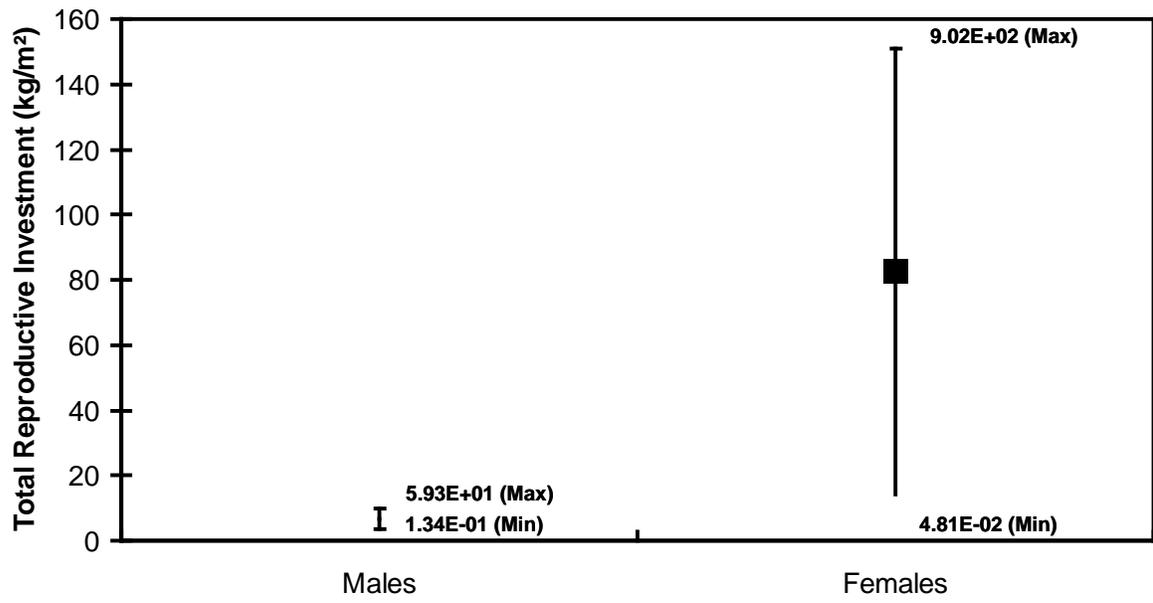


Figure 4

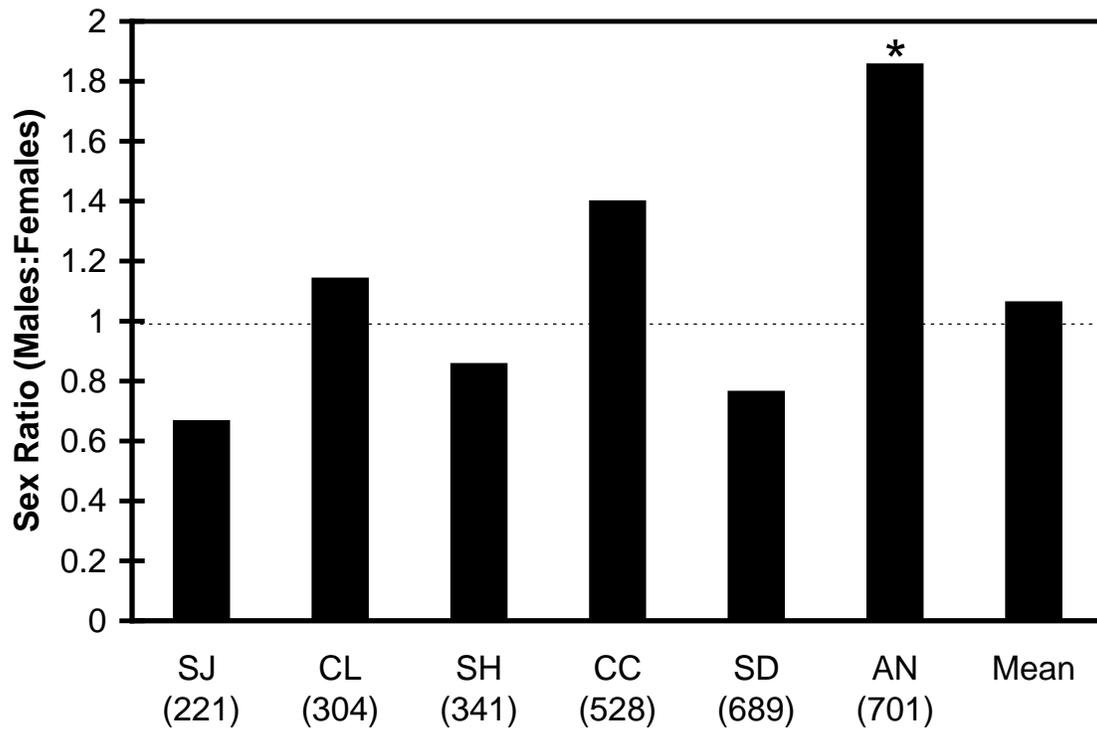


Figure 5

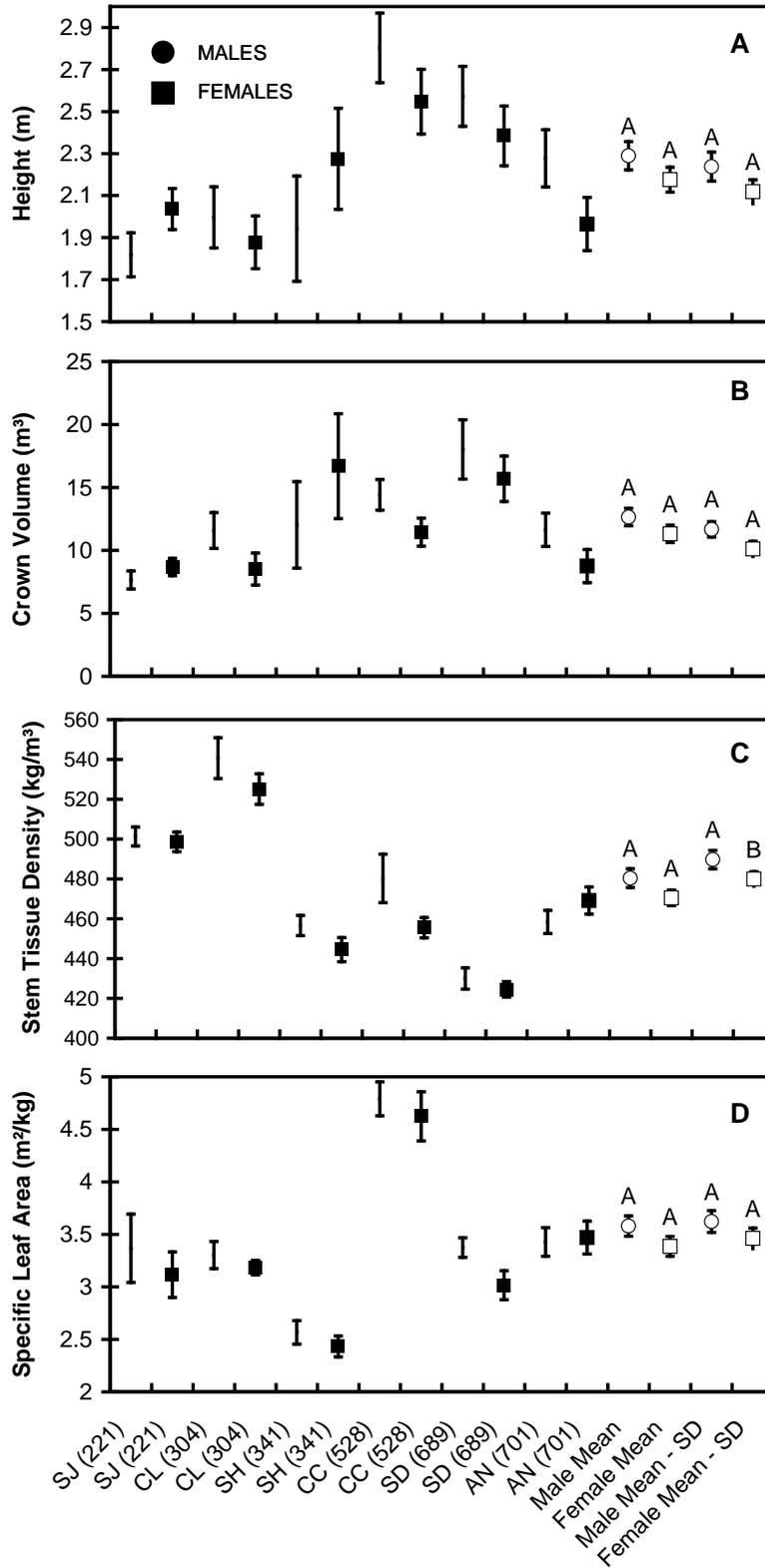


Figure 6

