

Sexual Dimorphism and Resource Allocation in Male and Female Shrubs of *Simmondsia chinensis*

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Summary. Desert populations of the evergreen dioecious shrub *Simmondsia chinensis* exhibit sex-related leaf and canopy dimorphisms not present in populations from more mesic coastal environments. Leaves on female shrubs have characteristically larger sizes, greater specific weights, and greater water-holding capacity than male leaves in desert habitats. In coastal scrub environments no significant difference is present, with leaf characteristics of both sexes similar to those of desert male shrubs. Desert female shrub canopies are typically relatively open with little mutual branch shading. In male shrubs canopies are more densely branched with considerable mutual shading of branches. Female plants allocate a greater proportion of their vegetative resources to leaves than do male plants. Considering total biomass, male plants allocate 10–15% of their resources (biomass, calories, glucose-equivalents, nitrogen, phosphorus) to reproductive tissues. Female allocation is dependent on seed set. At 100% seed set females would allocate 30–40% of their resources to reproduction, while female reproductive investment would equal that of males at approximately 30% seed set. Sexual dimorphism and the associated physiological characteristics in *Simmondsia* act as an alternative to differential habitat selection by male and female plants. Female plants respond to limited water resources in desert areas by increasing their efficiency in allocating limited resources to reproductive structures.

Introduction

Fruit production in plants is known to be a metabolically expensive process, requiring a large amount of available energy and nutrients. In dioecious species, differential selective pressures may operate on male and female plants because of the greater metabolic expenses for female plants (Freeman et al., 1976; Lloyd, 1973). Since females require more energy to produce fruits, they may evolve different adaptive strategies in the same environment. We predict that females with heavy metabolic investments in fruits evolve mechanisms which optimize water, carbon, and nutrient use for production in environments in which those factors are limiting. Such adaptive mechanisms may be expressed through differential habitat selection or through differential morphological or physiological adaptations.

Simmondsia chinensis (Link) Schneid. is a common dioecious evergreen shrub occurring in the Sonoran Desert and in adjacent

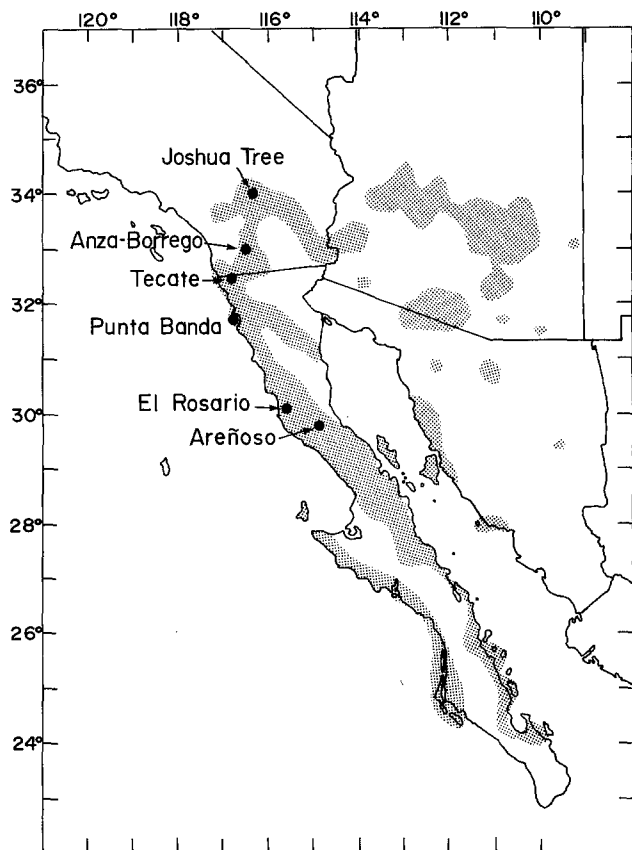


Fig. 1. Distribution of *Simmondsia chinensis* in the Sonoran Desert and adjacent Mojave Desert and coastal scrub of northwestern Baja California. Primary study sites are indicated. Adapted from Hastings et al. (1972)

parts of the Mojave Desert and semi-arid coastal scrub communities of northwestern Baja California (Fig. 1). The large fruit of this species contains a high content of liquid wax which has received considerable attention in recent years as a possible substitute for sperm whale oil (Gentry, 1958; Sherbrooke and Hasse, 1974; Yermanos, 1974). The production of heavy seed crops by female plants hypothetically produces a much greater reproductive cost for female than male *Simmondsia*, yet both water and nutrient availability are potentially limiting for productivity. In this paper we report on investigations of the differing selective pressures on shrubs of each sex of *Simmondsia*. We explore differential

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Methods and Material

Plant materials were analyzed for nutrient content at the Agricultural Research Station, University of Alaska, Palmer, Alaska. These analyses included nitrogen (micro-kjeldahl digestion of samples to ammonium-nitrogen analysis on Autoanalyzer II using indo-phenol procedure), phosphorus (nitric-perchloric acid digestion of tissue with Autoanalyzer II analysis using molybdenum blue method, ether extractives; see Allen et al., 1974), non-structural carbohydrates (see Allen et al., 1974), and hemicellulose (neutral detergent fiber minus acid detergent fiber), and cellulose and lignin (determination in acid detergent fiber with permanganate - see Van Soest and Wine, 1968).

Leaf samples obtained at the Joshua Tree site on four different occasions through 1977–1978 were used to determine mean leaf surface area for individual leaves, leaf specific weight (mg cm^{-2}) and water content ($\text{mg H}_2\text{O cm}^{-2}$) measurements for male and female plants. These measurements were also obtained from selected leaf samples of other populations: at Cottonwood Springs and Squaw Tank in Joshua Tree National Monument, at Borrego Springs and Yaqui Wells in Anza Borrego State Park, and at four locations in Baja California. Comparative water stress was obtained with a pressure bomb at Punta Banda and Yaqui Wells. Measures of leaf resistance to water loss were also obtained at these locations with a Lambda Corporation Model 60 Porometer. A Hitachi scanning electron microscope (SEM) was used to examine the leaf surfaces of male and female leaves.

	<i>n</i>	% male	% female
Mojave Desert			
Joshua Tree – north slope	32	45	55
south slope	40	48	52
Sonoran Desert			
Anza-Borrego			
-Borrego Springs	20	53	47
-Yaqui Wells	92	52	48
Arenoso	50	50	50
Northwestern Baja California			
Punta Banda	150	55	45
El Rosario	35	49	51

Population	\bar{x} Leaf surface area (cm ²)		Sample size	Significance level
	female	male	<i>n</i>	
Desert:				
Joshua Tree	3.83	1.98	70	$P < 0.0005$
Borrego Springs	4.95	2.53	20	$P < 0.01$
Cottonwood Springs	3.54	2.83	20	$P < 0.05$
Squaw Tank	3.35	2.16	20	$P < 0.005$
Yaqui Wells	3.09	2.35	20	$P < p.10$
Areñoso	3.43	2.45	20	$P < 0.001$
Coastal Scrub:				
Punta Banda	2.25	2.30	20	$P > 0.10$
Tecate	2.73	2.44	20	$P > 0.10$
El Rosario	2.92	2.89	20	$P > 0.10$

Sex ratios of populations of *Simmondsia chinensis* sampled in the southern Mojave Desert, western Sonoran Desert and coastal scrub of northwestern Baja California were all found to be very close to 50:50. At our Joshua Tree site north- and south-facing slopes were sampled individually to determine if microhabitat selection was occurring. Sex ratios were 45:55 male to female on the relatively more mesic north-facing slopes and 48:52 on the relatively more xeric south-facing slopes (Table 1). At Yaqui Wells in Anza Borrego State Park where *Simmondsia* occurs near the limits of its aridity tolerance on rocky south-facing slopes at a relatively low elevation, there may be a slight tendency for increased male survival. The sample size of stunted shrubs on this slope is too small, however, to statistically demonstrate any habitat selection. Less arid slopes in the same area show an even sex ratio (Table 1). Although Gentry (1958) reports sex ratios of 4:1 males to females for *Simmondsia* in Arizona, the sex ratios near Tucson are very close to 1:1 (Niall McCarten, personal communication).

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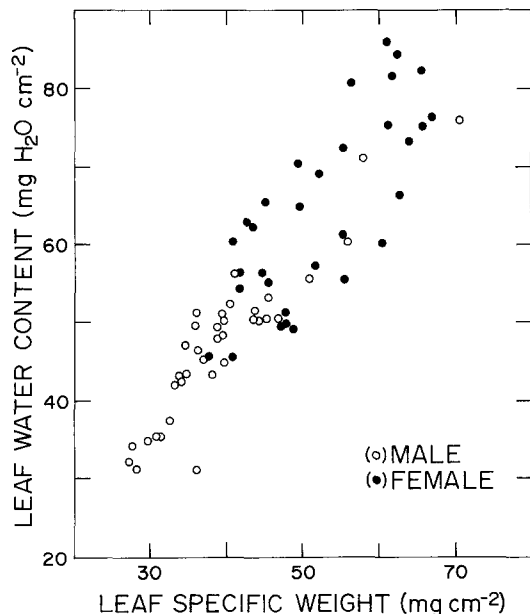


Fig. 2. Relationship of leaf water content to leaf specific weight in male and female leaves of *Simmondsia chinensis* at Joshua Tree, California

No evidence of differential microhabitat selection on the basis of substrate, drainage, or slope is present. Pressure bomb measurements of shrub water potential and porometer measurements of leaf conductance were carried out in May 1977 in coastal populations of *Simmondsia* at Punta Banda, Baja California, and in desert populations at Yaqui Wells, Anza Borrego State Park. No

significant differences between male and female shrubs were found for either water potential or leaf conductance. Water potentials were considerably lower (more stressful) in both populations than values expected from measurements reported by Al-Ani et al. (1972).

Although differential habitat selection does not appear to be occurring, a strong leaf dimorphism is evident in desert populations of *Simmondsia*. In six desert populations studied the leaves of female shrubs are significantly larger than those of males (Table 2). At Joshua Tree the mean female leaf size is 3.83 cm^2 in comparison to only 1.98 cm^2 for male leaves. Three other populations of *Simmondsia* surveyed, all in mediterranean-climate coastal scrub communities, show no significant difference in the leaf surface area between male and female shrubs. In these populations the surface area of male leaves is very similar to that of desert populations, while the female leaf is reduced (Table 2). Mean annual precipitation for coastal scrub communities typically varies from $180\text{--}250 \text{ mm yr}^{-1}$, in comparison to levels of $80\text{--}150 \text{ mm yr}^{-1}$ for the desert populations. Maximum seasonal water stress in coastal populations is considerably lower than in desert populations (Al-Ani et al., 1972).

Leaf dimorphism in *Simmondsia* is also evident in characteristics of leaf specific weight (g dry wt cm^{-2}) and water content of fresh leaves. In the Joshua Tree population mean leaf specific weight is 51.6 mg cm^{-2} , while male leaves are significantly lower in specific weight ($P 0.001$) with only 38.0 mg cm^{-2} . Mean leaf water content in March 1976 was 63.9 mg cm^{-2} for females and 46.4 mg cm^{-2} for males. The greater water contents characteristic of female leaves and concomitant greater leaf specific weights are not the result of any fundamental structural difference in leaves between the sexes, but rather represent the greater thickness of many female leaves. Relatively thick individual leaves from

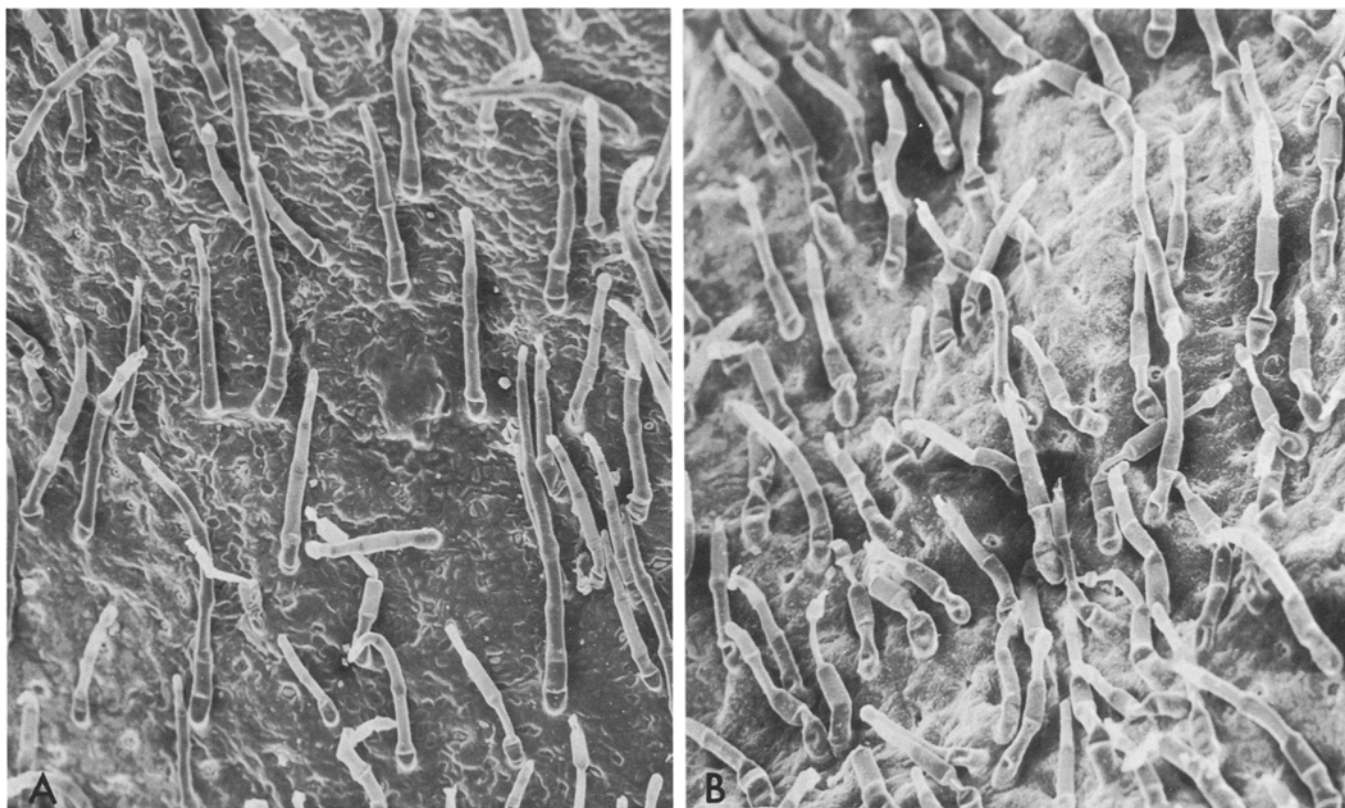


Fig. 3. SEM micrographs of upper leaf surface in *Simmondsia chinensis*: A. female leaf, $\times 50$ B. male leaf, $\times 50$

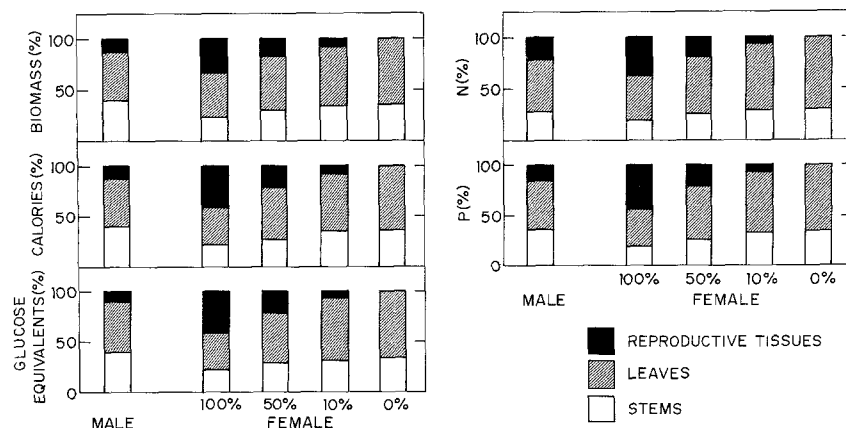


Fig. 4. Allocation of resources to reproductive tissues, leaves and stems in male and female shrubs of *Simmondsia chinensis* from Joshua Tree, California. Female data are shown for four levels of seed set

Table 3. Relative metabolic and nutrition costs of production of foliage branches for male and female *Simmondsia chinensis* at Joshua Tree, California, March, 1977

	Female (% total allocation)	Male (% total allocation)
Biomass		
stems	36.8	44.8
leaves	63.8	55.2
Calories		
stems	37.5	46.2
leaves	62.5	53.8
Glucose-equivalents		
stems	35.6	42.8
leaves	64.4	57.2
Nitrogen		
stems	32.5	36.0
leaves	67.5	64.0
Phosphorus		
stems	36.8	42.7
leaves	63.2	57.3

Table 4. Caloric and nutrient contents of above-ground biomass compartments in male and female *Simmondsia chinensis*. Data for shrubs at Joshua Tree, California, March 1977

	Female	Male
Energy content (cal g ⁻¹ air-dry wt)		
leaves	4466	4356
stems	4604	4637
reproductive tissues	5659	4958
Nitrogen (% dry wt)		
leaves	1.34	1.41
stems	1.11	0.98
reproductive tissues	1.46	2.33
Phosphorus (% dry wt)		
leaves	0.23	0.25
stems	0.23	0.23
reproductive tissues	0.32	0.38

male plants have the same pattern of specific leaf weight and water content as do female leaves of the same structure (Fig. 2). However, since female leaves in desert population do average a greater specific weights than male leaves, their water storage ability per unit of leaf area is greater than for males.

Preliminary analyses of leaf surface characteristics with a scanning electron microscope (SEM) indicate that leaf hair density and structure may differ between male and female leaves from desert populations (Fig. 3). Female leaves have lower densities of hairs than male leaves, while individual hairs on female leaves are frequently longer than those of males. The implications of these differences need further investigation but surface structures may provide a possible vegetative characteristic for separating male and female plants. Separation of sexes in the seedling stage would be immensely valuable for selecting female plants for agricultural use.

In addition to these patterns of leaf dimorphism, male and female *Simmondsia* in desert populations can usually be separated by a divergent geometry of canopy architecture. While shrub size does not differ significantly, female shrubs characteristically have an open canopy structure with fewer secondary branches than males and less mutual shading by individual branches. Male shrubs are typically much more densely branched with a larger number of small secondary branches and considerably more mutual shading within the canopy. For individual branches the leaf area index (LAI) of male and female shrubs is very similar, with values of 1.69 and 1.38 m² m⁻² respectively. For an entire canopy, however, the multilayers of branch structure in male shrubs produce a much higher LAI for males in comparison to females.

As indicated by the divergent patterns of canopy architecture, male and female *Simmondsia* differ considerably in their allocation of energy and nutrients to vegetative tissues. The relative metabolic and nutritional costs of production of foliage branches of each sex are shown in Table 3 for populations at Joshua Tree. Leaf biomass accounts for 64% of total vegetative material in females but only 55% in males. The ratio of leaf to stem biomass is 1.72 for females but only 1.23 for males, indicating a significantly increased allocation of vegetative resources of females into photosynthetic tissues. On a caloric basis females allocate 62% of vegetative resources into leaves against 54% in males. The caloric value for leaves and for stems do not differ significantly between the two sexes (Table 4). For estimated glucose-equivalents in production of vegetative tissues, the comparative values are 64% and 57% respectively for females and males. The two sexes allocate a very similar proportion of nitrogen to leaves (Table 3), reflecting a slightly higher mean nitrogen content in male leaves (Table 4).

When reproductive tissues are considered the pattern of relative allocation of metabolic and nutritional resources shows an even stronger pattern of divergence between the two sexes (Fig. 4). While male flowers are relatively small, they are much more numerous than female flowers and represent a considerable resource investment. For the five parameters of resources considered (i.e. biomass, calories, glucose-equivalents, nitrogen and phosphorus) males allocate 10–15% of each into reproductive tissues (Fig. 4). Female reproductive tissues, in comparison to male flowers, have significantly higher caloric content per unit of dry weight reflecting their liquid wax content, but a lower nitrogen and phosphorus content (Table 4). Since sepals make up only a very small percentage of the potential resource investment in a mature fruit, the pattern of allocation of resources in female plants is strongly dependent on the success of seed set. For this reason the relative allocation of resources in female plants is shown in Figure 4 for hypothetical seed sets of 100%, 50%, 10% and 0%, with calculations based on values in Table 3. For a 100% seed set the female plant would utilize 30–40% of its resources for reproduction. At lower seed sets this resource allocation becomes lower, with female reproductive investment equally that of males at approximately 30% seed set.

Discussion

While *Simmondsia chinensis* is characteristically a Sonoran Desert plant, its distribution shows a pattern of primary occurrence in areas where significant winter rainfall is present. Gentry (1973) reports that *Simmondsia* in Arizona responds only to winter and spring precipitation and is unable to utilize summer precipitation for growth. He further suggests that the species originated near the coast and has been limited in its migration eastward by cold temperature extremes. If this pattern is correct, then the sexual leaf and canopy dimorphisms described here may be viewed as selective adaptations of female individuals to stressful desert environments.

In coastal scrub environments of northwestern Baja California where populations of *Simmondsia* experience more abundant and predictable water resources, no significant leaf or canopy dimorphism was observable between female and male shrubs. Under the more stressful desert conditions of the range of the species a consistent pattern of significant sexual dimorphism is present. This dimorphism is evident in the production of larger leaves with higher specific weights and the allocation of relatively smaller amounts of metabolic and nutritional resources to stem material in female shrubs.

Differential selection on sexes of dioecious plants have been described in the past. Freeman et al. (1976) discuss differential habitat selection among male and female plants in five dioecious desert species. They found higher population ratios of female plants occurring in microhabitats of greater water availability while males were dominant on more xeric sites. Lloyd (1973) attributed male-skewed sex ratios in dioecious Umbelliferae to intraspecific competition with female plants outcompeted by males. Neither of these investigations noted sexual leaf or canopy dimorphisms in the species studied. The possibility of differential selection on male and female individuals of tropical tree species in Costa Rica has been discussed by Opler and Bawa (1978) and Melanpy and Howe (1978).

In *Simmondsia*, sexual dimorphism appears to act as an alternative to differential habitat selection in the populations we studied. Female plants respond to limited water resources in desert areas

by increased efficiency in allocating limited resources to reproductive structures. In comparison to male plants, females allocate fewer resources to stem structures without reducing photosynthetic surface area significantly for individual branches by increasing leaf size. At the scale of leaf dimensions involved, functional changes in leaf energy balance response do not occur with this increased size. On a total canopy basis females are able to allocate a greater amount of resources to reproductive structures by developing an open canopy with less vegetative biomass of both stems and leaves. In male shrubs selective pressures are lacking to alter the denser canopy structure characteristic of both sexes in coastal populations.

Greater leaf thickness in female plants in desert populations provides an added selective advantage. Since the water content per unit of leaf area is directly proportional to dry weight per unit area, this greater thickness provides a considerable benefit in increased water storage. Our measurements at Joshua Tree in March 1976 indicate that the total water content of a female leaf averaged 266% that of a male leaf. This is particularly significant in *Simmondsia* since leaf conductances are rather low in comparison to other woody desert species (Adams et al., 1977, 1978). Increased water storage ability should be particularly important to females since fruit production takes place relatively late in the growing season (later than male resource-allocation to reproductive structures) when water stress is greatest.

Differential selective pressures on male and female *Simmondsia* do not operate consistently. Seed set is notably variable from year to year in natural populations. In years of poor seed set the female reproductive effort may be less than that of males if lack of success is due to decreased pollination success. It is likely, however, that poor seed set results more often from environmental stress preventing either sex from allocating resources to reproductive structures. In good years where seed set may approach 100% there is no doubt that female reproductive expense far exceeds that of males (Fig. 4).

Since differential selective pressures on male and female shrubs is manifested in leaf and canopy dimorphisms in the desert populations we studied, it would not be surprising to find differential survival of the sexes at the most stressful extremes of the range of *Simmondsia*. We would expect that male plants should have increased drought tolerance due to their lower leaf to stem biomass ratio and smaller allocation of resources to reproductive structures. Such a prediction could explain the reported male-skewed sex ratios of *Simmondsia* in Arizona (Gentry, 1973). It is interesting to note that none of four recent investigations of drought stress in *Simmondsia* (Al Ani et al., 1972; Adams et al., 1977, 1978; Collatz, 1977) distinguished between male and female plants in their studies.

The phenomenon of leaf dimorphism in dioecious plants is not restricted to *Simmondsia*. The genus *Leucodendron* (Proteaceae) of the Cape Region of South Africa is characterized by larger leaves on female than male plants (Williams, 1972). These evergreen woody shrubs grow in a mediterranean-climate region notable for both water and low nutrient stress.

Previous data on the relative reproductive effort of male female plants of dioecious species are limited to a single example (Putwain and Harper, 1972). Future ecological and physiological investigations of dioecious plants should pay particular attention to the nature of possible differential selective pressures between male and female plants. These selective pressures will be most important in resource limited environments. While leaf dimorphism leaf size may be a generalized adaptation in evergreen perennials in water-stressed environment, other mechanisms of evolutionary re-

sponse may occur. Careful studies should consider morphological and physiological differences between sexes as well as differential habitat selection.

Acknowledgements. We thank Peter Tobiessen and Erik Scully for help in this investigation. F. Lynn Carpenter and Dennis O'Dowd provided helpful comments on a preliminary draft of this paper.

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Received March 9, 1979