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DIFFERENTIAL RESOURCE UTILIZATION BY THE SEXES
OF DIOECIOUS PLANTS

A Thesis

Presented to the

Department of Botany and Range Science

Brigham Young University

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

D. Carl Freeman

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This thesis, by D. Carl Freeman is accepted in its present form by the Department of Botany and Range Science of Brigham Young University as satisfying the thesis requirements for the degree of Master of Science.

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DIFFERENTIAL RESOURCE UTILIZATION BY THE SEXES
OF DIOECIOUS PLANTS

BY

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ABSTRACT

The distribution of male and female plants was examined in five dioecious, wind pollinated species representing five plant families and two classes (gymnosperms and angiosperms). The arid to semiarid habitats occupied by these species in northern Utah were stratified for sampling into two categories: chronically xeric and seasonally moist. Results show that for all species, males prevail on xeric microsites, while females dominate the more moist parts of each local environment. Habitat partitioning between the sexes is a strategy that maximizes seedset of females and pollen dispersal of males; it also tends to minimize intra-specific competition between the sexes.

Among animals, the importance of sexual dimorphism as a means of reducing intraspecific competition for resources has received considerable attention. Selander (1) found sexual dimorphism to be common among birds. Brown and Lasiewski (2) concluded that the phenomenon is an important attribute of elongate carnivores (such as weasels).

The question of differential resource utilization by male and female plants has apparently been little investigated, although Putwain and Harper (3) have described temporal differences in growth patterns of different sexed individuals of two dioecious (4) species of Rumex. Sex ratios within populations of dioecious plants have received more notice (3), but little attention has been directed toward the selective forces responsible for unbalanced ratios. In this study, we have observed the relative abundance of male and female individuals of five wind pollinated species along a strong environmental gradient. Our objective has been to determine whether environment exerts a significant influence on the proportion of males and females at selected points along a gradient of marked change in water availability. It is known that water availability can be modified by many factors (5): here we examine only salinity and topographic position as controlling variables.

Methods of sampling the populations varied according to species due to variation in plant size, population density and terrain. The sex of individuals of saltgrass [Distichlis stricta (Torr.) Rydb.], a grass commonly found in moist saline habitats,

was tallied within a series of 2.5 X 2.5 dm quadrats placed in habitats stratified into two salinity classes (Table 1). Sex of the nearest individual was also determined at 1 dm intervals along a transect which ran from a salt covered playa into a less saline meadow (Fig. 1).

Over 300 saltgrass individuals were sexed in the quadrats placed in habitats of differing salinity. Females were found to predominate on low salinity sites, while males dominated highly saline sites. The differential between males and females in respect to habitat preferences is highly significant (Table 1). The transect data shows males clustered near the more saline end of the transect while females are concentrated in the less saline portion of the study site (Fig. 1). The difference is again significant. It is thus apparent that male and female individuals of saltgrass are not randomly distributed in the environment but segregate according to microsite.

With meadow rue (Thalrictrum fendleri Engelm), a widely distributed herbaceous perennial of the buttercup family, the distribution of male and female plants was determined for entire local populations. Samples were taken in moist-shady and dry-sunny sites (Table 1). In addition, a line transect was run from a stream, through a wet meadow and up a dry hillside; sex of the nearest individual was noted at one meter intervals (Fig. 1).

These data were analyzed in the same manner as for saltgrass. The Chi-square test comparing distribution of sexes in moist-shady as opposed to dry-sunny sites show a departure from

random expectations that is significant at the .001 level. Males dominate dry sites; females are concentrated on more moist sites (Table 1). The mean distance of male individuals from the moist end of the transect is significantly greater (i.e., farther up the dry hillside) than that for females (Fig. 1). This difference is significant at the .05 level.

Boxelder (Acer negundo L.), a tree-size maple typically confined to streambeds in northern Utah, was sampled by counting the number of female and male plants along a stream and on adjoining slopes. Females dominate the stream banks; males prevail on the hillsides (Table 1). The difference is significant at the .001 level. It should be noted that females may dominate sites where the stream has meandered in the past, thus confusing the pattern to some extent, since pockets of females may exist away from the current streambed.

Mormon tea (Ephedra viridis Coville), a gymnospermous, desert shrub occurring on rocky slopes intermixed with big sagebrush (Artemisia tridentata Nutt.) and bitterbrush [Purshia tridentata (Pursh.) DC.], was sampled by sexing all individuals in populations on steep slopes and adjacent alluvial bottom-lands. Males of Mormon tea are found in greater numbers on steep slopes, while females are more common on better watered sites at the base of the slopes. A Chi-square test indicates that the difference is significant at the .001 level (Table 1). Female plants may occur on steep slopes, but there they usually grow where large boulders increase the runoff available to them.

Shadscale [Atriplex confertifolia (Torr. & Fern.) S. Wats.], a saltbush of arid, saline soils, was sampled along transects; nearest individuals were sexed at five meter intervals. The proportion of male and female plants was determined along transects placed on the tops and edges of knolls and on alluvial fans at the base of such knolls in the juniper [Juniperus osteosperma (Torr.) Little]-big sagebrush vegetation zone. As Table 1 illustrates, there is a significant difference ($P < .05$) between the distribution of sexes on the two sites. Males are most abundant on ridges, while females are relatively better represented on the moister alluvial fans.

Shadscale was also sampled on different topographic positions in the greasewood [Sarcobatus vermiculatus (Hook.) Torr.]-shadscale zone, a habitat more xeric than and about 8 km removed from the juniper-sagebrush zone mentioned above. The elevational difference between the two sampling zones was approximately 30 m. The two sampling sites within the greasewood-shadscale zone were separated by 3 m in elevation and were 500 m apart. The more xeric, higher elevation site is dominated by shadscale and Indian ricegrass [Oryzopsis hymenoides (R. & S.) Riker]; the lower site where runoff water accumulates is dominated by greasewood and shadscale. As shown in Table 1, there is again a marked difference in the distribution of sexes between xeric and better watered sites. Females are better represented on the moister sites.

The distribution of male and female individuals of shad-scale was also compared between the juniper-sagebrush and the greasewood-shadscale zone (topographic subsamples were pooled for each zone). Results show that females outnumber males in the more mesic juniper-sagebrush zone, but males prevail in the more xeric greasewood-shadscale zone (6). The difference is significant at the .001 probability level.

Our data demonstrate conclusively that the sex ratio of populations of these five dioecious species change significantly within short distances. Those changes are correlated with marked changes in the environment, particularly with respect to available soil moisture. The mechanism by which the sexes are segregated is unknown, but at least two hypotheses can be formulated. Sivtsev and Sizov (7) report that for six dioecious species (including Acer negundo), males were consistently less sensitive to water stress than females. It thus seems possible that there is differential survival of male and female individuals along a gradient of available soil moisture. Other data (8,9) imply that the sex of individuals of some dioecious species is not irrevocably fixed genetically, but is dependent upon subtle environmental variation. Our data offer no basis for determining which, if either, of these hypotheses best explains the observed segregation of sexes.

Regardless of the causal mechanism, it seems apparent that the observed environmental separation of the sexes of these wind pollinated species imparts advantages to both sexes. Males on windy, sparsely vegetated topographic sites almost certainly

contribute more genetic material to the next generation than do males on densely vegetated, depressional sites; wind is more likely to reach and effectively disperse the pollen of the former individuals. Since effective precipitation in the area of study is concentrated in the winter period (10) and pollen of all species studied is dispersed within a few weeks after growth initiation, drought should not strongly depress the reproductive potential of males.

Reproductive output of females, however, is dependent on a much longer period of favorable soil moisture conditions than that of males. Furthermore, female reproductive efforts require the largest input of resources during the driest part of the year, long after pollen production has ceased. Additionally, seed production demands the investment of many times more resources than are required for pollen production. Consequently, females on better watered and more fertile sites can be expected to contribute more genetic material to subsequent generations than females on xeric sites.

Given such a differential in reproductive success of male and female individuals on xeric as opposed to more predictably mesic sites, disruptive selection (11) within a common gene pool seems inevitable. For males, a linkage between genes for maleness and tolerance of exposed, chronically droughty sites might be expected to evolve. Conversely, among females, genes conferring adaptability for better watered sites should become linked with those for sex. Such selection would be especially beneficial when

spatial segregation of the sexes arises through differential survival of male and female seedlings on sites of variable aridity.

Disruptive selection operating as outlined above would tend to maximize the reproductive efficiency of dioecious species. The process not only adapts each sex for that site where it will most effectively contribute to the perpetuation of the species, but it also tends to minimize competition between males and females of the same species.

Intraspecific competition may be especially deleterious in dioecious species, since any reduction in number and/or size of seeds set by the female as a consequence of competition will reduce not only her contribution to the next generation but that of the competing male as well (since the male's genes can be represented in the next generation only through the female). Thus by competing with the female, the male's genetic contribution to the next generation is inescapably reduced. The magnitude of such intraspecific competition is controlled by the ratio of males-to-females in the population and other autecological parameters. For three of the species considered here (i.e., saltgrass, Mormon tea, and shadscale), intraspecific competition would be expected to be an important selective force, since communities dominated by these species are commonly of low diversity (indeed saltgrass meadows approach monocultures). Consequently much and in some cases most of the interindividual competition among these species is generated by members of the same species.

We postulate that the adverse effects of intraspecific competition will tend to complement and reinforce disruptive selection.

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10. U.S. Department of Commerce, "Decennial Census of United States Climate--Utah," Climatology of the United States No. 81-37 (1962). Only 42% of the annual precipitation in northcentral Utah falls during the growing season (April-September), a time of great evaporative stress.
11. Stebbins, G. L., "Flowering Plants, Evolution Above the Species Level," Belknap Press of Harvard Univ. Press, Cambridge, Mass. (1968), p. 10. We define disruptive selection as the diversification of a homogenous genepool into at least two more or less distinct genotypes.

Table 1. The influence of site on sex ratio in populations of five species. The Chi-square tests are based on 2x2 contingency tables with 1 degree-of-freedom.

	Male	Female	Male/Female Ratio
<u>Saltgrass</u>			
Very saline	77	26	2.96
Moderately saline	81	138	.59
	Summation $\chi^2 = 39.99^{***}$		
<u>Meadow Rue</u>			
Dry-sunny	210	31	6.77
Moist-shady	23	94	.24
	Summation $\chi^2 = 157.82^{***}$		
<u>Box Elder</u>			
Dry-sunny	68	51	1.33
Moist-shady	22	47	.47
	Summation $\chi^2 = 11.17^{***}$		
<u>Mormon Tea</u>			
Steep slope lands	105	67	1.57
Bottom lands	27	97	.28
	Summation $\chi^2 = 44.98^{***}$		
<u>Shadscale</u>			
Within Juniper-Sagebrush Zone			
Top of knoll	40	60	.67
Alluvial bottom	19	56	.34
	Summation $\chi^2 = 4.13^{**}$		
Within Greasewood-Shadscale Zone			
Drained slope	59	40	1.48
Bottom lands	21	29	.72
	Summation $\chi^2 = 4.14^{**}$		
Between Zones			
Greasewood-Shadscale	80	69	1.17
Juniper-Sagebrush	59	116	.51
	Summation $\chi^2 = 13.15^{***}$		

*** Significant to the .001 level

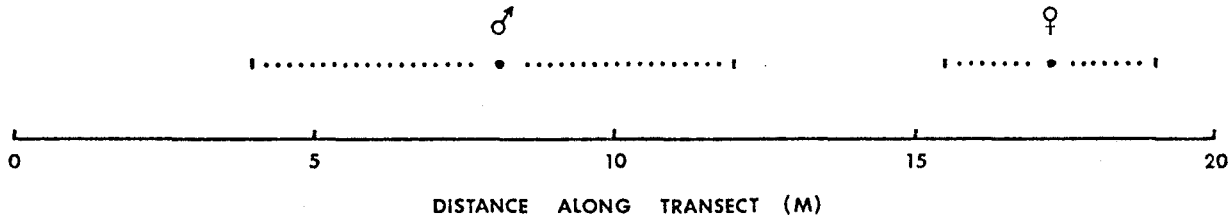
** Significant to the .05 level

Fig. 1. The average and standard deviation of distances of male (♂) or female (♀) individuals of saltgrass and meadow rue along transects running from areas of moisture stress to moisture abundance. Distances are measured from the left in both cases.

SALTGRASS

HIGH
SALINITY

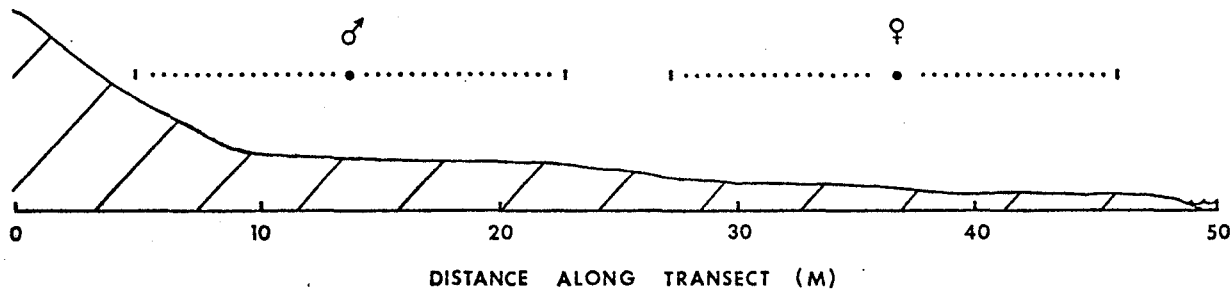
LOW
SALINITY



MEADOW RUE

DRY
SUNNY

MOIST
SHADY



APPENDIX

LITERATURE REVIEW

Reproductive biology has appealed to investigators from diverse disciplines, consequently many facets have received considerable attention, while others have remained virtually virgin. It is not surprising that Darwin did extensive research in this area. If one examines Darwin's book, "The Various Forms of Flowers on Plants of the Same Species," one will find case histories of heterostylous, polygamous, monoecious and dioecious plants, and hypotheses concerning their origin. Darwin (1889) also discusses many aspects of pollination ecology. However, it remained for Knuth (1895) to publish the monumental pollination ecology work of the 19th century.

Reproductive biology was largely the domain of the empiricist during the 19th century, but in the 1920's several investigators began to numerically analyze population growth (Lotka 1922, Pearl 1925, Volterra 1926). They found that population growth could be approximated closely by an equation with but two constants (provided that no predation or interspecific competition took place). The basic equation was as follows: $dN/dt = rN(K-N)/K$ where N is the number of individuals in the population, K , the carrying capacity of the population, and r is defined as the birth rate minus the death rate. This has been termed the logistic growth equation.

There were various modifications proposed, but population theory did not significantly advance the work of Lotka and Volterra until 1954 when Cole analyzed the iteroparous, and semelparous strategies. He also analyzed the effect of the age of first reproduction and the contribution of progressively larger litters on population growth rate (r). His conclusions were that a semelparous species could achieve the same reproductive potential of an iteroparous species by increasing the number of offspring by one. He further concluded that r was greatly affected by the age of first reproduction and that each successive offspring would contribute less to the reproductive potential of the population than its older sibling.

Another major theoretical advance came in 1967, when MacArthur and Wilson proposed that natural selection tended to operate on the constants of the logistic growth equation. According to their theory, organisms can be divided into two reproductive strategy groups (albeit with some intergradation). The first group, r -strategists, are organisms with high reproductive rates. These organisms are usually short lived and devote a large portion of their biomass to reproduction. Only a small energy expenditure is made per offspring, however. Furthermore, these organisms are usually typified as pioneer species and are poor competitors. The k -strategist on the other hand devotes only a small fraction of its biomass to reproduction, but there is a high energy expenditure per offspring and therefore few offspring. These species tend to be long lived, good competitors and are typically climax species.

Pianka (1972), Gadgill and Solbrig (1972) and many others have marshalled a considerable amount of data supporting this theory.

The most useful aspect of the MacArthur-Wilson theory was in predicting the outcome of competition between two species depending upon the competition coefficients and the differing values of k , it being tacitly assumed that r played no part in the outcome of competition. Vandermeer (1975) has convincingly demonstrated that the above assumption is an artifact of the mathematical manipulation. He has refined and generalized the basic theory. The theory is not sufficiently general to cover all of reproductive biology. Indeed it only sheds light on the energetics of reproduction, and the consequences of each reproductive strategy.

The balance of this review will deal with the strategy of dioecy. Darwin (1889) posed the problem that I wish to deal with when he stated the following, "There is much difficulty in understanding why hermaphrodite plants should ever have been rendered dioecious." In general, dioecy has attracted many investigators who probed the genetic consequences of the habit, but have ignored the evolutionary forces responsible for its origin. Literature sources indicate that 22% of the trees in Costa Rican rain forests are dioecious (Bawa and Olper, 1975); 27% of the Hawaiian flora is dioecious (Carlquist 1966, Gilmartin 1968), and about 26% of the trees in Malayan rain forests are dioecious (Ashton 1969). These values stand in sharp contrast to the values of 2% of the British flora (Lewis 1942) and 3% of the California flora (Baker 1967) for dioecy. Yampolsky and Yampolsky (1922) report that only 5% of the

genera world wide are dioecious, and Lewis (1942) reports that only 5% of the species world wide are dioecious.

The dioecious habit has been studied widely from either a pure taxonomic point of view (Proctor 1971) or from a strictly genetic standpoint (Westergaard 1958; Winge 1929; Warmke 1946a, 1946b, 1946c; Warmke and Blakesle 1939a, 1939b, 1940). These and other studies have contributed a significant amount of data but have not identified the selective forces responsible for the origin of the dioecious habit. Nor are those forces elucidated by those that try and trace evolutionary lines. Darwin (1889) and Ornduff (1966) have postulated that dioecy may have arisen from heterostyly. Others have postulated that the dioecious plants arose from either perfect flowers or from gynodioecious plants (Connor 1973). These hypotheses are interesting but fail to identify the evolutionary force responsible for the fragmenting of bisexual parental stock into separate sexed populations.

If one wants to gain insight into the causal forces responsible for the dioecious habit, one must return to Darwin. Concerning the conversion of flowers from the perfect to the dioecious state, Darwin (1889) stated that, "There would be no such conversion, unless pollen was already carried regularly by insects or by wind from one individual to another; for otherwise every step toward dioeciousness would lead towards sterility." The thesis Darwin presents next is interesting and a theme to which we will return later. "As we must assume that cross-fertilization was assured before an hermaphrodite could be changed into a dioecious plant, we may conclude that the conversion has not been effected for the sake

of gaining the great benefits which follow from cross-fertilization." This statement is in sharp conflict with Levin (1975) who maintains that natural selection has favored dioecy because of genetic advantages imparted from outcrossing. Continuing with Darwin's argument, "we can, however, see that if a species were subjected to unfavourable conditions from severe competition with other plants, or from any other cause, the production of the male and female elements and the maturation of ovules by the same individual, might prove too great a strain on its powers, and the separation of the sexes would then be highly beneficial."

An alternative hypothesis has been provided by Levin (1975). He argues that "the persistent tracking of plant hosts by multiple pathogens and herbivores is a prime factor which prohibits the congealing of the genomes of species especially those in closed communities." The argument is based upon the premise that an open recombination system would be favored in a population which suffers from intense pest pressure due to a multitude of pathogens or herbivores.

The existence of Whittaker's (1969) evolutionary dance between pathogen and host has been adequately demonstrated in the last few decades. The belief has been widely held that all one had to do was incorporate a resistance gene into the genome of agricultural plants and the pathogen problem would disappear. As Day (1973, 1974) has adequately shown, when this is done, new virulent strains of the pathogen appear from the decedents of those few genetic deviants able to circumvent the defense mechanism of the host. Thus the dance begins, and the host must then change its

genome, thus forcing the pest to readapt if it is to survive. Levin (1975) argues that this process occurs in nature and may well be responsible for the high percentage of dioecy found in the tropics (dioecy being assumed to maximize outcrossing and consequent genetic recombinations). While Levin does not state that pest pressure is responsible for the evolution of dioecy in the tropics, the inference is clear.

Levin (1975) argues most convincingly that there is a greater pest pressure in the tropics. As I have noted above, high percentages of dioecy in the tropics has been documented by many workers. Certainly dioecy would maximize outcrossing and impart great genetic heterogeneity to the offspring. Such genetic diversity would be advantageous to green plants being tracked by pathogens and herbivores. Levin's (1975) hypothesis is too recent to be tested adequately, but that is hardly true for Darwin's (1889).

Darwin's hypothesis assumes that the physiological state of the plant influences its reproductive behavior. Modern work supports that hypothesis. Davidyan (1970) has reported that Gibberellin can alter the growth and the sex of hemp "D" plants. Arnoux and Mathiev (1969) have further demonstrated that "the environment can alter the sexual phenotype" of hemp. The environmental variables Arnoux and Mathiev referred to were photoperiod and/or moisture regimes. That sex could be reversed in hemp is somewhat surprising, since it has been reported to have distinct sex chromosomes (Westergaard 1958). Such results suggest that in

species where perfect, polygamodioecious, and dioecious flowered populations exist, the environment may play a strong role.

There are also indications that the physiology of males and females may be quite different with respect to resource partitioning. While sex reversal may not take place, there exists a partitioning of the environment along a resource gradient. Sivtzen and Sizou (1971, 1973) have shown in several common dioecious plants including Acer negundo that the males can tolerate a significantly greater water stress.

There are many modes of determining sex (Westergaard 1958) and sex ratios in dioecious plants; not all of them are environmentally determined. Lloyd (1974a, 1974b, 1974c, 1975). Michell (1973), and Wiens and Barlow (1975) have greatly expanded the knowledge of gametic selection and the cytological processes involved. Putwain and Harper (1972) argued that the sex ratio in Rumex acetossella and R. acetosa is the result of frequency dependent selection. But the effect of the environment on sex ratios has not received much attention.

It has been accepted that when a population becomes dioecious, total seed production will decline, since a portion of the population is male and thus sets no seed. There is evidence to support that conclusion, but there are indications that seed size is larger for dioecious as opposed to perfect flowered species. Larger seed size may increase seedling success and thus partially offset the consequences of reduced seed set. Connor (1973) demonstrated in Cortaderra of the Graminae that seeds from the dioecious females were significantly larger than those of hermaphrodites of

the same species. A similar observation was made over eighty years ago by Sir J. E. Smith (Darwin 1889) who reported the seed from female Serratula tincotorin plants to be larger than that of hermaphroditic individuals.

The literature thus suggests that the physiological state of the plant may well determine the sex in some species. It also seems apparent that the effect of the environment on sex ratios and the ultimate origin of dioecy has largely been ignored. Levin's (1975) postulate that pest pressure led to the evolution of dioecy cannot be accepted. The plant does not "know" apriori that dioecy will increase outcrossing. The laws of inheritance which govern the breeding system are subject to natural selection. Therefore, if the environment in which dioecous plants exist is carefully examined, one may well discover the forces which render plants dioecious.

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DIFFERENTIAL RESOURCE UTILIZATION BY THE SEXES
OF DIOECIOUS PLANTS

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ABSTRACT

The distribution of male and female plants was examined in five dioecious, wind pollinated species representing five plant families and two classes (gymnosperms and angiosperms). The arid to semiarid habitats occupied by these species in northern Utah were stratified for sampling into two categories: chronically xeric and seasonally moist. Results show that for all species, males prevail on xeric microsites, while females dominate the more moist parts of each local environment. Habitat partitioning between the sexes is a strategy that maximizes seedset of females and pollen dispersal of males; it also tends to minimize intra-specific competition between the sexes.

COMMITTEE APPROVAL: