

Aldo-keto reductases exist in all mammalian species analyzed and are found in submammalian species such as chickens, turkeys, and fungi (Table 1). Because of their wide distribution in tissue and their ability to metabolize normally occurring substrates (7, 8, 14, 20, 21), it is likely that aldo-keto reductases function in some ordinary capacity in cellular metabolism. These enzymes catalyze glucuronic acid reduction (14), crotonyl CoA reduction (6), aldose reduction (21), β -hydroxylated phenylethyl aldehyde reduction (5), and possibly other reactions. Since enzymes from different species display many similarities, comparative biochemical studies may substantiate the functional role of the catalysts.

The aldo-keto reductases function in detoxification to eliminate the chemically reactive carbonyl groups. Carbonyl reduction is a rapid, one-step pathway that simultaneously eliminates these reactive groups, modifies molecular polarity, and prepares the drug molecule for conjugation.

The alcohol metabolites resulting from carbonyl reduction of drugs usually retain pharmacologic activity (12, 19, 20). But an important modulating factor to activity is the stereochemical configuration of the alcohol product. Stereochemical configuration is determined by enzyme specificity and should be a prime consideration in drug design. The presence of a carbonyl group in a drug increases the variability in activity and possibly the toxicity through this biotransformation potential.

Certainly the similarities of the aldo-keto reductases from mammalian tissues are unlikely to be a matter of chance. From the cited collected studies it appears there is a system of related cytoplasmic aldo-keto reductases similar in several characteristics. These enzymes may be related genetically and through evolution, but these points remain for study.

NICHOLAS R. BACHUR

Laboratory of Clinical Biochemistry,
Baltimore Cancer Research Center,
National Cancer Institute,
3100 Wyman Park Drive,
Baltimore, Maryland 21211

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Differential Resource Utilization by the Sexes of Dioecious Plants

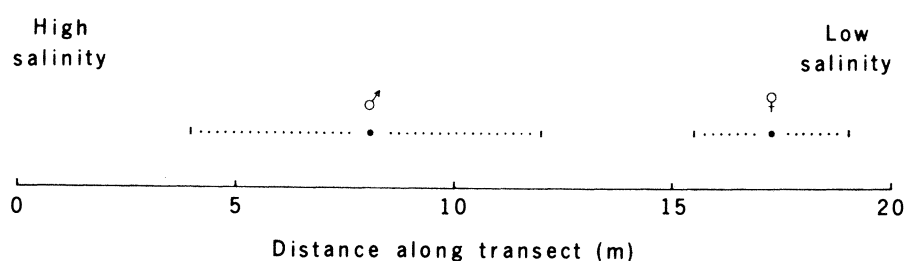
Abstract. *The distribution of male and female plants was examined in five dioecious, wind-pollinated species representing five plant families and two classes (gymnosperms and angiosperms). The arid to semiarid habitats occupied by these species in northern Utah were stratified for sampling into two categories: chronically xeric and seasonally moist. The results show that for all species, males are more abundant on xeric microsites, while females are overrepresented on the moister parts of each local environment. Differential distribution of the sexes along a soil moisture gradient is a strategy that maximizes seed set of females and pollen dispersal of males; it also tends to minimize intraspecific competition between the sexes.*

The importance of sexual dimorphism in animals as a means of reducing intraspecific competition for resources has received considerable attention (1, 2). 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).

In contrast, the question of differential resource utilization by male and female plants has apparently been little investigated, although Putwain and Harper (3) described temporal differences in growth

patterns of male and female 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 determining the selective forces responsible for unbalanced ratios. 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

Salt grass



Meadow rue

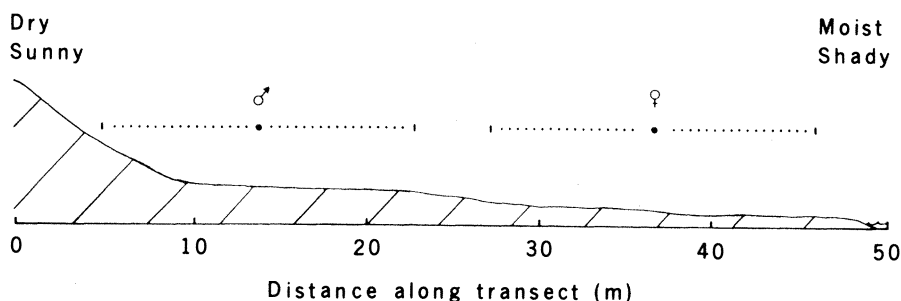


Fig. 1. Averages and standard deviations of distances of male (♂) and female (♀) individuals of salt grass and meadow rue along transects running from areas of moisture stress to moisture abundance. Distances are measured from the left in both cases.

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); in this report we examine only salinity and topographic position as controlling variables.

Methods of sampling the populations varied according to species because of variations in plant size, population density, and terrain. The sex of flowering stalks of salt grass [*Distichlis spicata* (L.) Greene var. *stricta* (Torr.) Beetle], a grass commonly found in moist saline habitats, was tallied within a series of quadrats (2.5 by 2.5 dm) placed in habitats stratified into two salinity classes (Table 1). The sex of the nearest inflorescence was also determined at 1-dm intervals along a transect which ran from a salt-covered playa into a less saline meadow (Fig. 1).

More than 300 salt grass inflorescences were sexed in the quadrats. Females were proportionately more abundant than males on low-salinity sites, while the reverse was true on highly saline sites. These differences are highly significant (Table 1). The transect data show males clustered near the more saline end of the transect and females 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 salt grass are not randomly distributed in the environment but segregate according to microsite.

With meadow rue (*Thalictrum 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; the sex of the nearest individual was noted at 1-m intervals (Fig. 1).

These data were analyzed in the same manner as for salt grass. The chi-square test comparing distribution of sexes in moist, shady as opposed to dry, sunny sites shows a departure from random expectation that is statistically significant. Males are most abundant on dry sites; females are concentrated on moister sites (Table 1). The mean distance from the moist end of the transect is significantly greater for males than for females (Fig. 1); this difference is significant at $P = .05$.

Box elder [*Acer negundo* L. var. *interior* (Britt.) Sarg.], a tree-size maple typi-

cally confined to stream beds in northern Utah, was sampled by counting the numbers of female and male plants along a stream and on adjoining slopes. There are proportionately more females along the stream banks than on the adjacent hillsides (Table 1). It should be noted that females may be concentrated on sites where the stream has meandered in the past, which confuses the pattern to some extent, since pockets of females may exist away from the current stream bed.

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) D.C.], was sampled by sexing all individuals in populations on steep slopes and adjacent alluvial bottoms. 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 (Table 1).

Table 1. Influence of site on sex ratio in populations of five species. The chi-square tests are based on two-by-two contingency tables with 1 degree of freedom.

Environment	Male (No.)	Female (No.)	Male/ female
<i>Salt grass</i>			
Very saline	77	26	2.96
Moderately saline	81	138	0.59
	$\Sigma\chi^2 = 39.99^{**}$		
<i>Meadow rue</i>			
Dry, sunny	210	31	6.77
Moist, shady	23	94	0.24
	$\Sigma\chi^2 = 157.82^{**}$		
<i>Box elder</i>			
Dry, sunny	68	51	1.33
Moist, shady	22	47	0.47
	$\Sigma\chi^2 = 11.17^{**}$		
<i>Mormon tea</i>			
Steep slope lands	105	67	1.57
Bottomlands	27	97	0.28
	$\Sigma\chi^2 = 44.98^{**}$		
<i>Shadscale</i>			
Juniper-sagebrush zone			
Top of knoll	40	60	0.67
Alluvial bottom	19	56	0.34
	$\Sigma\chi^2 = 4.13^*$		
Greasewood-shad- scale zone			
Drained slope	59	40	1.48
Bottomlands	21	29	0.72
	$\Sigma\chi^2 = 4.14^*$		
Between zones			
Greasewood- shadscale	80	69	1.17
Juniper-sagebrush	59	116	0.51
	$\Sigma\chi^2 = 13.15^{**}$		

**Significant at $P = .01$.

*Significant at $P = .05$.

Shadscale [*Atriplex confertifolia* (Torr. & Fern.) S. Wats.], a saltbush of arid, saline soils, was sampled along transects; nearest individuals were sexed at 5-m 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 distributions 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 at 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 difference in elevation 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 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 shadscale was also compared between the juniper-sagebrush and greasewood-shadscale zones (topographic subsamples were pooled for each zone). The results show that females outnumber males in the more mesic juniper-sagebrush zone, but the reverse is true in the more xeric greasewood-shadscale zone (6). The difference is statistically significant.

Our data demonstrate that the sex ratios of populations of these five dioecious species change significantly within short distances. The changes are correlated with marked changes in the environment, particularly with respect to available soil moisture. The mechanism by which the unequal sex ratios arise is unknown, but at least two hypotheses can be formulated. Sivtsev and Sizov (7) reported 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 on subtle environmental variations. Our data offer no basis for determining which, if either, of these hypotheses best explains the observed tendency for the sexes to be differentially represented on sites of varying soil moisture availability.

Regardless of the causal mechanism, it seems likely that the observed environmental separation of the sexes of these wind-pollinated species increases the reproductive contribution of the average adult of either sex. 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 the pollen of all species studied is dispersed within a few weeks after growth initiation, drought should not strongly depress the reproductive potential of males.

The reproductive output of females, however, is dependent on a much longer period of favorable soil moisture conditions than is 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 offspring to subsequent generations than females on xeric sites.

With 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 if sex is rigidly controlled by genetics. In males, genes for maleness and tolerance of exposed, chronically droughty sites might be expected to become associated. Conversely, among females, genes conferring adaptability for better-watered sites should become associated with those for sex. Such an association of genes should make each sex competitively superior on its preferred site to the other sex and thus provide a mechanism for the observed spatial distribution of the sexes (12). Such differential survival of individuals would be expensive for both sexes. Control of sexual expression

by environmental variation would appear to be more economical.

When the tendency for the sexes to be spatially separated arises through differential survival of seedlings, the spatial pattern can be expected to reduce intraspecific competition between reproductively active adults. The reproductive potential of dioecious species should be increased by a resource-partitioning scheme in which males occupy marginal sites and compete minimally with females on better sites (13). For three of the species considered here (salt grass, Mormon tea, and shadscale), male-female competition would be expected to be an important selective force, since communities dominated by these species are commonly of low diversity (indeed, salt-grass meadows approach single-species stands). Consequently, much and in some cases most of the competition these species experience is intraspecific. In at least these cases, we postulate that the adverse effects of competition between the sexes tend to complement and reinforce disruptive selection pressures arising from differential success of males and females on xeric and moist sites.

D. CARL FREEMAN

Department of Botany and Range
Science, Brigham Young University,
Provo, Utah 84602

LIONEL G. KLIKOFF

Department of Biology,
Allegheny College,
Meadeville, Pennsylvania 16335

KIMBALL T. HARPER

Department of Botany and Range
Science, Brigham Young University

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10. Environmental Data Service, *Climatology of the United States No. 81-37* (Government Printing Office, Washington, D.C., 1962). Only 42 percent of the annual precipitation in north-central Utah falls during the growing season (April to September). The relative effectiveness of that moisture for plant growth is greatly reduced by rapid evaporation.
11. G. L. Stebbins, *Flowering Plants, Evolution Above the Species Level* (Harvard Univ. Press, Cambridge, Mass., 1968), p. 10. We define disruptive selection as the diversification of a homogenous gene pool into at least two distinct genotypes.
12. This type of argument also offers a possible explanation for the origin of the dioecious habit from monoecious or polygamous parental stock that is wind-pollinated. The argument need not be limited to water availability; any limiting resource that differentially affects male and female reproductive success could trigger a disruptive selection process that could eventually result in partial or complete separation of the sexes.
13. Intraspecific competition may be especially deleterious to dioecious species, since any reduction in the number or size of seeds set by the female as a consequence of competition from males 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).
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Histones and G Banding of Chromosomes

Abstract. Polylysine, polyarginine, and histones H1, H2A, H2B, and H3 inhibit Giemsa staining and chromosome banding by binding to DNA and preventing side stacking of the positively charged thiazine dyes to the negatively charged phosphate groups on DNA. This is a nonspecific effect and does not of itself provide evidence for a role of histones in G banding. The question of whether histones are involved in chromosome banding is reviewed.

The G banding (1) of chromosomes is a widely used procedure, but the mechanism is poorly understood. Since the bands correlate well with the chromomeres of pachytene chromosomes (2), the banding procedures are essentially enhancing a preexisting structural component of the chromosomes. The bands are produced in fixed metaphase chromosomes by various protein denaturing procedures, followed by staining with Giemsa, a mixture of thiazine dyes plus eosin. Since the treatment of chromo-

somes with acid to remove histones does not result in banding, but subsequent treatment with trypsin does, it has been suggested that histones are not directly involved (3-5). It has recently been proposed that the removal of histone fractions H1 and H2A from fixed chromosomes is involved in the induction of G bands because these fractions, when exogenously applied at low concentrations, inhibit banding (6). The H2B and H3 histones did not inhibit banding and were supposedly not so involved. We re-