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Patterns of phenotypic variation and sexual size dimorphism in *Rumex acetosa* and *R. acetosella*

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Abstract

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The patterns of phenotypic variation and sexual dimorphism in height and dry weight were examined in populations of *Rumex acetosa* and *R. acetosella*, and the interactions between phenotypic variation, sexual dimorphism, sex ratio and various environmental variables were explored. In both species, more markedly in *R. acetosa*, the sex ratios were commonly female-biased. The lower level of phenotypic variation often observed in males is suggested to result from a greater physiological tolerance in variable environments. Females are the taller sex in *R. acetosa* and *R. acetosella*. The correlations between the degree of sexual size dimorphism and the proportion of females were found to be significantly positive. It is proposed that the reason for sexual size dimorphism in *Rumex* is an ecological mechanism which is based on the interaction between mortality differences and size distribution. Taller plants have lower mortality, and this feature is more important for females which have higher resource demands in reproduction than do males.

Key words: Phenotypic variation, sexual dimorphism, sex ratios, *Rumex*.

Introduction

In dioecious species males and females have different roles in the reproductive biology and also different resource requirements, which could cause selection pressures leading to the evolution of sexual dimorphism. All secondary sex characters between sexes in structures other than the primary sex organs and sex-associated phenological differences are generally called collectively sexual dimorphism. Such sexual differentiation has been observed in a number of dioecious plants (for a review, see Lloyd and Webb 1977). Traditional studies on sexual dimorphism in plants have often been limited to floral characteristics. More recently there have been reports on other aspects of sexual dimorphism in morphological and physiological traits as well as in ecological features such as life history parameters and resource allocation patterns (e.g. Wallace and Rundell 1979, Bullock and Bawa 1981, Bawa et al. 1982, Meagher 1984, Ågren 1987). Sexual dimorphism may influence both population structure and breeding patterns in dioecious species.

Putwain and Harper (1972) have suggested for *R. acetosella* that differences in such secondary characteristics as flowering time, inflorescence height and dry weight may represent differentiation between the sexes in utilization of environmental resources. Niche differentiation could result in the reduction of between-sex competition and the stabilization of the sex ratio. However, Lloyd and Webb (1977) postulate that differences in secondary sex characters in plants are of selective value directly in relation to the distinct roles of males and females in sexual reproduction. Since plants are nonmotile, the ecological consequences of sexual dimorphism have been shown to be sometimes expressed as spatial segregation of the sexes along some environmental gradient (e.g. Freeman et al. 1976, Grant and Mitton 1979, Onyekwelu and Harper 1979, Meagher 1984, Vitale and Freeman 1986).

The sorrels *Rumex acetosa* and *R. acetosella* are dioecious perennial weeds which exhibit a very plastic above-ground morphology (e.g. Farris and Schaal 1983, Korpelainen, pers. obs.). In *R. acetosella* Harris (1970) found the growth forms to vary from a compact, prostrate form in the open subalpine habitat to a taller form occurring in more closed and shaded habitats. Farris and Schaal (1983) have shown that in *R. acetosella* the observed differences among populations are the result of phenotypic plasticity rather than genetic differentiation. Such plastic response to the environment may help to explain how *R. acetosa* and *R. acetosella* can exist in a wide range of environments. Both species are capable of vegetative reproduction, and particularly in *R. acetosella* populations may almost exclusively be maintained by vegetative reproduction in some habitats (Putwain et al. 1968). Due to vegetative reproduction, each genet (genetic individual) may be composed of one or several genetically identical ramets. *R. acetosa* and *R. acetosella* possess morphologically distinguishable sex chromosomes (Westergaard 1958), which means that sex determination is genetic instead of being environmental.

In this study I examine the patterns of phenotypic variation, separately for males and females, and sexual dimorphism in height and biomass in populations of *R. acetosa* and *R. acetosella* living in a range of habitats, and explore the relationship between phenotypic variation, sexual dimorphism, sex ratio and environmental variables. Since male and female plants have different roles in reproduction in dioecious species, they may react differently to variable environments. This can be expressed as sexual dimorphism and differences between the sexes in the level of phenotypic variation. In addition to exploring these patterns of population and environmental variables, I attempt to find an evolutionary explanation for the observed phenomena.

Materials and methods

Six populations of *Rumex acetosa* and twelve populations of *R. acetosella* inhabiting a range of environmental conditions were studied during the growing seasons of 1988–89. All populations are located in Central Finland in the counties of Jäppilä (62°20′N 27°30′E) and Varkaus (62°20′N 27°50′E). For the four populations of *R. acetosa* originating from Jäppilä I use the abbreviations J1–J4, and for the two populations originating from Varkaus I use the codes V1 and V2. Similarly, the five populations of *R. acetosella* located in Jäppilä are coded J1–J5, and the seven populations from Varkaus have the abbreviations V1–V7. In one case only the two species coexisted in the same habitat, J2 of *R. acetosa* and J5 of *R. acetosella*. The population J4 of *R. acetosa* was included in the study only in 1989. The pairwise distances of the populations of *R. acetosa* varied from 0.3 km to 21 km, except for the populations J1 and J2 which were located only 100 meters apart but occupied distinct habitats. In *R. acetosella* the pairwise distances ranged from 0.7 km to 22 km. Soil samples from the sites of the *Rumex* populations were analyzed for pH and the content of calcium, magnesium, nitrogen, phosphorus and potassium by Viljavuuspalvelu Oy in Helsinki.

Populations were studied twice during each growth season: First in June at the time of flowering (early June for *R. acetosa* and late June for *R. acetosella*), and then two months later when the seeds were mature. At both times the sex and the height of each ramet in the sample were recorded. Most populations were relatively small in size. In those cases all ramets were examined. The sample sizes are shown in Table 1. In August of both years, all the plants recorded in June were harvested, dried at 95 °C for 24 hours, and their dry weight was determined.

To study the patterns of phenotypic variation separately in males and females, the height and the above-ground biomass (dry weight) were recorded and the coefficient of variation (the standard deviation expressed as a percentage of the mean) was calculated for each sample and for the weighted averages across populations. To test if males and females differed in the amount of phenotypic variation in height and dry weight, the differences in the coefficient of variation between the sexes were tested by means of a t test (Sokal and Brauman 1980). Measuring dry weight instead of height is a better means of comparing plant sizes in *Rumex* because of the great variation in their growth forms.

To test spatial and temporal variation in phenotypic variation, the differences between and within populations at different times in the variance of height and weight in males and females were determined by means of a Bartlett's test of homogeneity (Steel and Torrie 1980), when more than two variances were compared, and by means of a F test (Sokal and Rohlf 1987), when two variances were compared. Differences in height and weight between females and males were tested by a t test (Sokal and Rohlf 1987). Before testing the significance of differences in the variances of height and weight, the data were tested for normality (Sokal and Rohlf 1987) and found to follow the normal distribution.

Results

The patterns of phenotypic variation

In *Rumex acetosa* the ramet sex ratios were always strongly female-biased, while the sex ratios of *R. acetosella* expressed considerably more variation (Table 1). Ramet sex ratios were used rather than genet sex ratios because it is problematic to recognize which ramets belong to the same genet. More details of the pattern of temporal and spatial sex ratio variation and the mechanisms responsible for the observed sex ratio variation in *Rumex* populations are given in Korpelainen (1991).

On average, the females of *R. acetosa* possessed considerably more variation than males in height and weight in 1988 (Table 2). In 1989 the level of phenotypic variation was more equal. In *R. acetosella* females expressed a significantly higher level of phenotypic variation in late summer samples. In June samples, when only height was measured, even a few cases with a higher level of phenotypic variation in males were detected though the averages across populations were equal.

The amount of phenotypic variation in height and weight varied significantly between populations (Table 3). Also considerable temporal changes in phenotypic variation within populations were detected. Out of the 65 within-population tests in height and weight in both sexes 50 tests indicated a significant temporal change in the level of phenotypic variation.

Sexual size dimorphism

To examine the degree of sexual size dimorphism in greater detail, the ratios of average female height per average male height and average female dry weight per average male dry weight were determined. Table 4 gives the average level of sexual size dimorphism, the range of variation between populations and the significance of differences in

Tab. 1. The ramet sex ratios of six populations of *Rumex acetosa* and twelve populations of *R. acetosella* located in Central Finland (data from Korpelainen 1991). Sex ratios are expressed as a proportion of females to the total. The sample sizes are in parentheses.

Species	Population	Sex ratio			
		June 1988	August 1988	June 1989	August 1989
R. acetosa	J1	0.59 (365)	0.82 (266)	0.62 (368)	0.79 (154)
	J2	0.94 (218)*	0.95 (133)*	0.70 (542)*	0.74 (367)*
	J3	0.66 (510)*	0.84 (149)*	0.61 (508)*	0.84 (37)*
	J4	–	–	0.88 (296)*	0.78 (108)*
	V1	0.88 (241)	0.82 (264)	0.91 (170)	0.84 (269)
	V2	0.87 (55)*	0.78 (59)*	1.00 (32)*	0.55 (29)*
R. acetosella	J1	0.48 (263)*	0.67 (105)*	0.39 (127)*	–
	J2	0.70 (490)	0.48 (162)	0.51 (271)	–
	J3	0.38 (654)*	0.67 (106)*	0.62 (257)*	0.77 (141)*
	J4	0 (578)*	0.17 (101)*	0.06 (193)*	0.62 (94)*
	J5	0.58 (343)*	0.49 (105)*	0.42 (501)*	0.62 (268)*
	V1	0.62 (687)*	0.91 (229)*	0.57 (333)*	0.58 (93)*
	V2	0.18 (562)*	0.20 (126)*	0.09 (117)*	0.54 (94)*
	V3	0.65 (990)	0.64 (160)	0.58 (306)	0.79 (212)
	V4	0.49 (814)	0.65 (268)	0.52 (172)*	0.59 (163)*
	V5	0.90 (276)*	0.90 (70)*	0.73 (66)*	0.55 (159)*
	V6	0.51 (600)*	0.40 (96)*	0.40 (474)*	0.44 (34)*
	V7	0.81 (320)*	0.81 (203)*	0.45 (153)*	0.72 (146)*

* Denotes a sex ratio determined by counting the entire population.

Tab. 2. The weighted average heights, weights and standard deviations for female and male ramets, and the numbers of populations with equal coefficient of variation ($s/\bar{x}$) and with significantly ($P < 0.05$) higher coefficient of variation in females or in males. The symbols < and > express the direction of significant differences ($P < 0.05$) in the average values of coefficient of variation (a t test). In single-population comparisons only samples with more than 10 ramets of one sex are included.

Species	Trait	Season	Average ± SD		$s/\bar{x}$ (no. populations)		
			Females	Males	Equal	Higher in females	Higher in males
R. acetosa	Height (cm)	June 1988	77.5 ±19.5 >	55.1 ±12.6	2	2	0
		August 1988	77.6 ±19.7 >	69.4 ±14.8	2	1	1
		June 1989	69.9 ±16.2	50.1 ±11.3	3	2	0
		August 1989	68.5 ±14.8	62.4 ±14.4	5	0	0
	Weight (g)	August 1988	0.91 ± 0.69	0.57 ± 0.34	3	1	0
		August 1989	0.70 ± 0.46	0.53 ± 0.35	5	0	0
R. acetosella	Height (cm)	June 1988	36.5 ±11.2	28.8 ± 9.0	7	1	3
		August 1988	36.3 ±11.1 >	34.4 ± 8.1	8	3	0
		June 1989	30.7 ±10.2	29.5 ± 9.7	7	1	3
		August 1989	27.3 ± 8.1	27.6 ± 8.3	8	2	0
	Weight (g)	August 1988	0.19 ± 0.17 >	0.13 ±0.09	11	1	0
		August 1989	0.12 ± 0.11 >	0.12 ±0.09	8	2	0

Tab. 3. The significance of variation between populations in the variance of height and weight in females and males (Bartlett's test of homogeneity).

Species	Trait	Season	Significance	
			Females	Males
R. acetosa	Height	June 1988	P<0.001	n.s.
		August 1988	P<0.05	P<0.001
		June 1989	P<0.001	P<0.001
		August 1989	P<0.001	P<0.001
	Weight	August 1988	n.s.	P<0.001
		August 1989	P<0.001	P<0.001
R. acetosella	Height	June 1988	P<0.001	P<0.001
		August 1988	P<0.001	P<0.001
		June 1989	P<0.001	P<0.001
		August 1989	P<0.001	P<0.001
	Weight	August 1988	P<0.001	P<0.001
		August 1989	P<0.001	P<0.001

Tab. 4. Weighted average sexual size dimorphism (SSD) and the range of variation, expressed as a ratio of average female and male ramet height and dry weight, and the significance of differences in the average female and male size (a t test). In single-population comparisons only samples with more than 10 ramets of one sex are included.

Species	Trait	Season	SSD (range)	Significance of size difference
R. acetosa	Height	June 1988	1.31 (1.10–1.37)	P<0.001
		August 1988	1.12 (0.97–1.20)	P<0.001
		June 1989	1.34 (1.07–1.42)	P<0.001
		August 1989	1.10 (0.83–1.25)	P<0.001
	Weight	August 1988	1.60 (1.51–1.75)	P<0.001
		August 1989	1.32 (0.71–2.16)	P<0.001
R. acetosella	Height	June 1988	1.27 (1.00–1.47)	P<0.001
		August 1988	1.06 (0.81–1.33)	P<0.001
		June 1989	1.04 (0.92–1.28)	P<0.01
		August 1989	0.99 (0.88–1.17)	n. s.
	Weight	August 1988	1.44 (0.64–2.26)	P<0.001
		August 1989	1.05 (0.67–1.53)	n. s.

the average female and male sizes. The results show that sexual size dimorphism was more extensive in *R. acetosa* than in *R. acetosella*, and that the size difference between the sexes was greater when measured as dry weight than when measured as height. In both species the degree of height differences between the sexes decreased toward late summer almost to the point of disappearing. However, the dry weight differences, which were measured only in August samples, show that sexual size dimorphism still exists in late summer populations.

Interactions between population and environmental variables

Interactions between phenotypic variation, sexual size dimorphism, sex ratio and environmental variables were examined by calculating correlation coefficients between the coefficients of variation of height and dry weight, the degree of sexual size dimorphism, several soil characteristics, population density and sex ratio, separately for June 1988–89 and August 1988–89 samples of *R. acetosa* and *R. acetosella* (Tables 5 and 6). Most populations contributed two data points to the correlations, one from the year 1988 and the other from the year 1989. This was justified as the population variables examined here expressed considerable between-year variation.

The relations between the level of phenotypic variation and environmental variables and between the degree of sexual size dimorphism and environmental variables appeared to be of little importance. In *R. acetosa* significant negative correlation coefficients were found between the coefficient of variation of male height in June an the levels of nitrogen and phosphorus. Also in females, considerable but not statistically significant negative correlations were observed between those variables. No such correlations were detected in *R. acetosella*, in which the only significant environmental correlation was the negative correlation between the coefficient of variation of female dry weight and the level of calcium in August samples. However, even by chance alone a few significant correlations are expected to be found.

No statistically significant density effects on the level of phenotypic variation or on sexual size dimorphism were detected in either *Rumex* species. Still, in *R. acetosa*, especially in early summer, the amount of phenotypic variation appeared to be somewhat greater at high population densities.

The relation between the amount of phenotypic variation and sex ratio proved to be inconsistent. In the June samples of *R. acetosa* males expressed a significant negative correlation between the coefficient of variation of height and sex ratio, which means that males have less variation when the sex ratio is more female-biased. In females the situation was similar but not significant. In late summer the situation changed, and the correlations between the coefficient of variation and sex ratio were positive but non-significant, except for the correlation between the coefficient of variation in female dry weight and dry weight sex ratio (= the total dry weight of females divided by the total dry weight of all individuals in the sample). In *R. acetosella* the correlation coefficients between the amount of variation in height and sex ratio were significantly positive in the August samples.

The correlations between the degree of sexual size dimorphism and the amount of phenotypic variation showed an inconsistent pattern. However, the interaction between size dimorphism and sex ratio appeared important in both *Rumex* species. The results indicating a positive correlation between those variables were clear in August samples. The situation in early summer was not certain since the size of the plants was then measured as height only, which is not as good a measure for size as is dry weight. In order to explore the observation more thoroughly I formed a regression between the ramet sex ratio and the natural logarithm of female dry weight per male dry weight for August samples of *R. acetosa* and *R. acetosella* (Figs. 1 and 2). The regression lines for both species had significantly positive slopes. The result is that the sex ratios of *Rumex* populations are more extremely female-biased when the size difference between the sexes is greater toward taller females. In *R. acetosa* and *R. acetosella* the degree of sexual size dimorphism, when expressed as a dry weight ratio between females and males, explains 66% and 28%, respectively, of the variation in the ramet sex ratio. However, in the case

Tab. 5. Correlations between coefficient of variation ($s/\bar{x}$) of ramet height and dry weight and the degree of sexual size dimorphism, soil characteristics, population density and sex ratio in *Rumex acetosa,* based on the combined data of 1988–89. The significance is indicated by $*0.01 < P < 0.05$, $**0.001 < P < 0.01$, $***P < 0.001$. The degrees of freedom in parentheses.

Trait	Height (June)			Height (August)			Dry weight (August)		
	Females $s/\bar{x}$	Males $s/\bar{x}$	Size dimorphism	Females $s/\bar{x}$	Males $s/\bar{x}$	Size dimorphism	Females $s/\bar{x}$	Males $s/\bar{x}$	Size dimorphism
Soil characteristics									
pH	−0.058 (8)	−0.511 (6)	−0.568 (6)	0.199 (8)	0.618 (6)	0.366 (6)	0.228 (8)	0.450 (5)	0.619 (5)
Ca	0.444 (8)	0.681 (6)	0.049 (6)	0.221 (8)	0.035 (7)	0.328 (6)	0.222 (8)	0.084 (5)	0.655 (5)
K	−0.558 (8)	−0.595 (6)	0.013 (6)	−0.151 (8)	0.098 (6)	−0.098 (6)	0.013 (8)	−0.012	−0.332 (5)
Mg	−0.095 (8)	−0.171 (6)	0.290 (6)	−0.102 (8)	−0.081 (6)	−0.472 (6)	−0.315 (8)	0.515 (5)	−0.026 (5)
N	−0.614 (8)	−0.784 (6)*	−0.338 (6)	−0.174 (8)	0.214 (6)	−0.046 (6)	0 (8)	−0.257 (5)	−0.611 (5)
P	−0.540 (8)	−0.791 (6)*	−0.551 (6)	−0.009 (8)	0.649 (6)	0.188 (6)	0.111 (8)	0.153 (5)	−0.050 (5)
Population density (June)	0.569 (9)	0.564 (7)	0.413 (7)	–	–	–	–	–	–
Population density (August)	–	–	–	0.351 (9)	0.032 (7)	0.076 (7)	0.492 (9)	0.517 (6)	0.215 (6)
Ramet sex ratio (June)	−0.544 (9)	−0.850 (7)**	−0.363 (7)	–	–	–	–	–	–
Ramet sex ratio (August)	–	–	–	0.285 (9)	0.021 (7)	0.684 (7)*	0.512 (9)	0.398 (6)	0.690 (6)
Dry weight sex ratio (August)	–	–	–	0.355 (9)	−0.134 (7)	0.764 (7)*	0.611 (9)*	0.320 (6)	–
Size dimorphism	−0.203 (7)	0.703 (7)*	–	0.140 (7)	−0.205 (7)	–	0.272 (6)	0.010 (6)	–

Tab. 6. Correlations between coefficient of variation ($s/\bar{x}$) of ramet height and dry weight and the degree of sexual size dimorphism, soil characteristics, population density and sex ratio in *Rumex acetosella,* based on the combined data of 1988–89. The significance is indicated by $*0.01 < P < 0.05$, $** 0.001 < P < 0.01$, $*** P < 0.001$. The degrees of freedom in parentheses.

Trait	Height (June)			Height (August)			Dry weight (August)		
	Females $s/\bar{x}$	Males $s/\bar{x}$	Size dimorphism	Females $s/\bar{x}$	Males $s/\bar{x}$	Size dimorphism	Females $s/\bar{x}$	Males $s/\bar{x}$	Size dimorphism
Soil characteristics									
pH	0.030 (21)	0.043 (22)	−0.112 (21)	0.198 (21)	0.047 (19)	0.015 (19)	0.137 (21)	−0.963 (19)	0.101 (19)
Ca	−0.225 (21)	0.200 (22)	0.045 (21)	−0.234 (21)	−0.189 (19)	−0.185 (19)	−0.554 (21)**	−0.246 (19)	−0.236 (19)
K	−0.327 (21)	−0.168 (22)	−0.201 (21)	−0.388 (21)	−0.254 (19)	−0.289 (19)	−0.341 (21)	0.048 (19)	−0.343 (19)
Mg	0.025 (21)	0.304 (22)	0.138 (21)	−0.176 (21)	0.002 (19)	−0.286 (19)	−0.311 (21)	0.025 (19)	−0.228 (19)
N	−0.014 (21)	0.109 (22)	0.008 (21)	−0.170 (21)	0.070 (19)	0.064 (19)	−0.272 (21)	0.056 (19)	−0.112 (19)
P	−0.097 (21)	0.193 (22)	0.108 (21)	−0.300 (21)	−0.240 (19)	−0.180 (19)	−0.341 (21)	−0.046 (19)	−0.310 (19)
Population density (June)	0.023 (21)	−0.002 (22)	0.318 (21)	–	–	–	–	–	–
Population density (August)	–	–	–	−0.161 (21)	0.058 (19)	−0.059 (19)	0.139 (21)	0.142 (19)	−0.062 (19)
Ramet sex ratio (June)	0.329 (21)	0.140 (22)	0.401 (21)	–	–	–	–	–	–
Ramet sex ratio (August)	–	–	–	0.422 (21)*	0.652 (19)**	0.543 (19)*	0.312 (21)	0.221 (19)	0.511 (19)*
Dry weight sex ratio (August)	–	–	–	0.408 (21)	0.584 (19)**	0.574 (19)**	0.238 (21)	0.090 (19)	–
Size dimorphism	0.086 (21)	0.219 (21)	–	0.330 (19)	0.430 (19)	–	0.103 (19)	−0.118 (19)	–

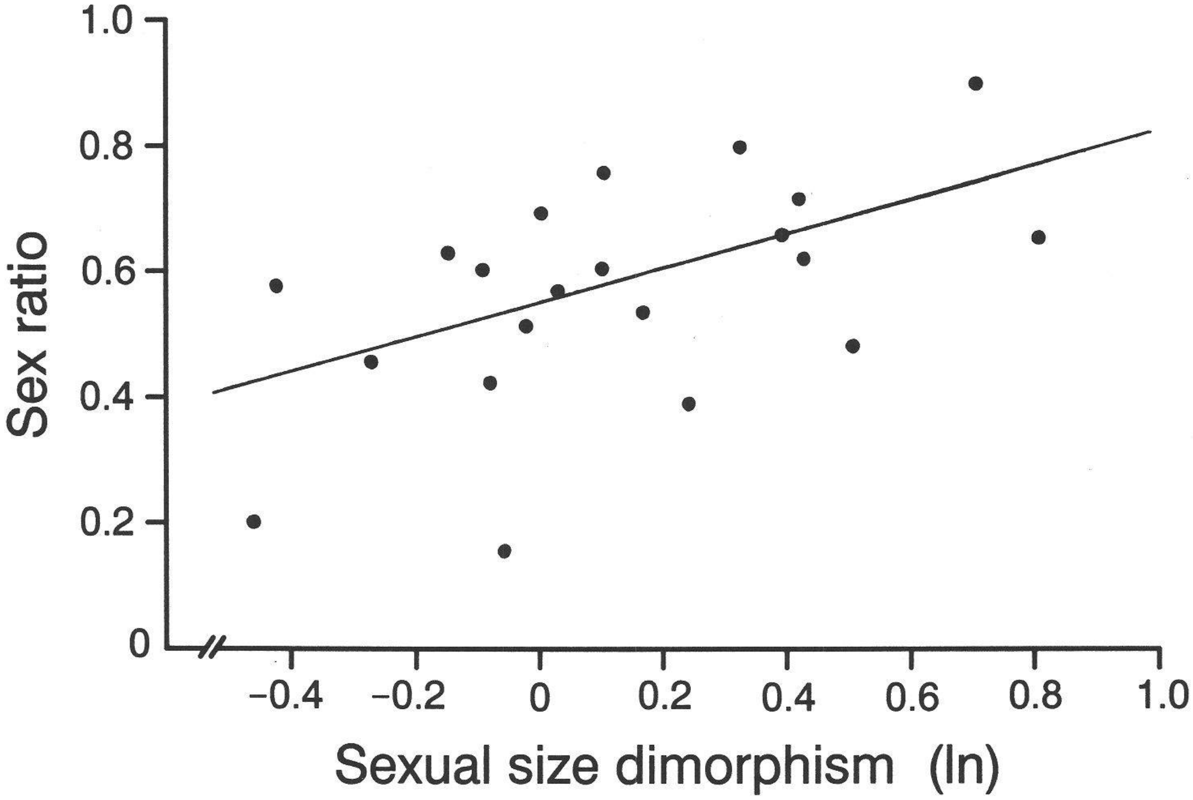

Fig. 1. Ramet sex ratio plotted against sexual size dimorphism in *Rumex acetosa*. Sex ratios are expressed as a proportion of females to the total. The regression line is shown. The slope is significantly positive ($F_{(1,6)} = 11.38$, $P < 0.05$, $R^2 = 0.66$).

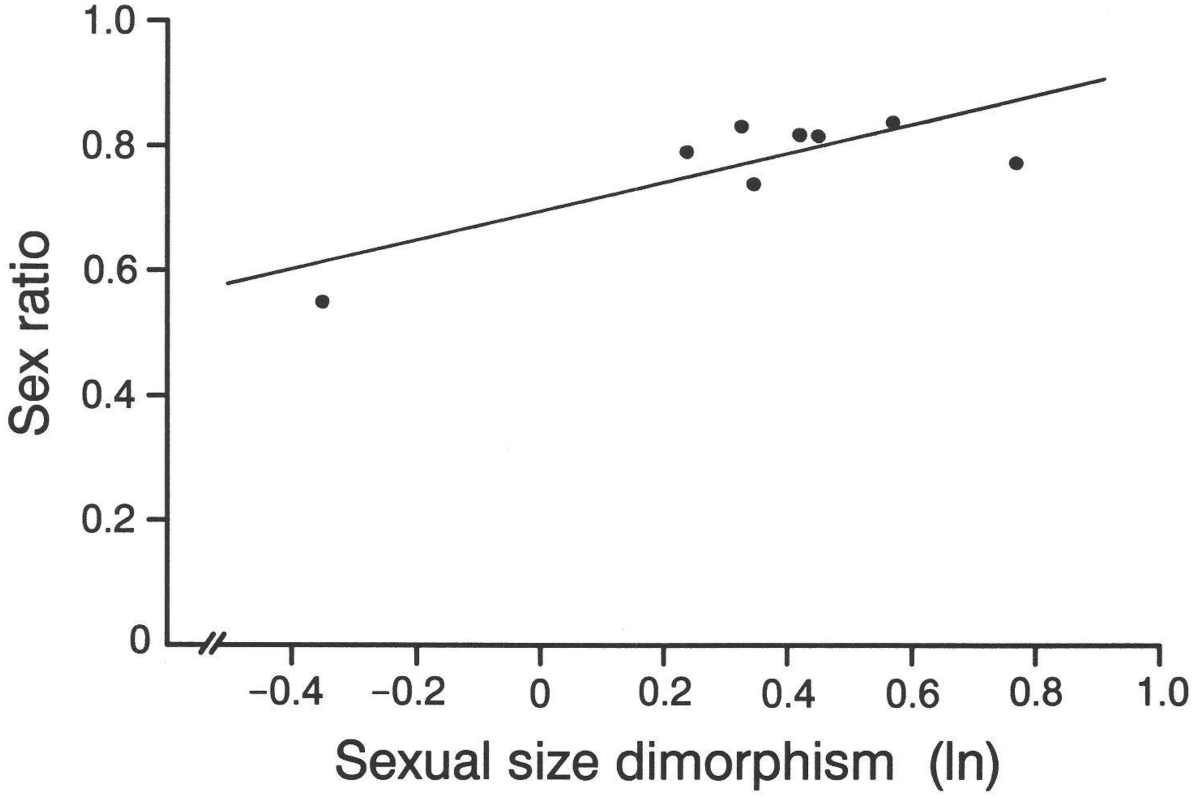

Fig. 2. Ramet sex ratio plotted against sexual size dimorphism in *Rumex acetosella*. Sex ratios are expressed as a proportion of females to the total. The regression line is shown. The slope is significantly positive ($F_{(1,19)} = 7.23$, $P < 0.05$, $R^2 = 0.28$).

of *R. acetosa* it is important to notice that the sample V2 of August 1989 strongly influences the relationship between sex ratios and sexual size dimorphism. If V2 of August 1989 is excluded from the study, the correlation and regression formed between sex ratios and the degree of sexual size dimorphism become nonsignificant. The low level of variation in sex ratios and the degree of sexual size dimorphism cause difficulties in drawing conclusions of the relationship between these two variables in *R. acetosa*.

Discussion

It is expected that plastic responses in growth should be the rule in species, such as *Rumex acetosa* and *R. acetosella*, which inhabit a range of environmental conditions. Both genetic and environmental components contribute to the resulting level of phenotypic variation.

A nongenetic component of phenotypic variation may be classified as random or systematic (Bull 1987). Random environmental variation describes variation that is uncorrelated with external factors. Phenotypic plasticity, in which the phenotype varies systematically with some environmental cue, is the other form of environmental variation. Although environmental effects are themselves not heritable, the susceptibility to them potentially is. The norm of reaction, that is the amount by which the expressions of a genotype are changed by different environments, is a measure of the plasticity of the characters in question. There are many situations where the plasticity of a character can have considerable adaptive significance. However, the definition of phenotypic plasticity does not imply that plastic responses are necessarily adaptive (Schlichting 1986).

Both males and females of *R. acetosa* and *R. acetosella* were found to possess considerable amounts of phenotypic variation. The lower level of phenotypic variation often observed in males when compared to females indicates that males are physiologically more tolerant to variation in the environment and they can manage in a wider range of environments with less decline of their performance. At first this seems to contrast with the commonly observed female predominance in *Rumex* populations. I suggest that females possess characteristics (e.g. lower mortality) which often make them superior to males. However, females, which have higher energy requirements in reproduction than do males, may suffer from harsh environmental conditions more easily than do males. Thus the female strategy involves a higher phenotypic plasticity while the male strategy includes a greater physiological tolerance and a more constant phenotype. However, the possibility that the lower level of phenotypic variation in males could be due to canalization or to differences in genetic correlations among traits can not be rules out.

Both in *R. acetosa* and *R. acetosella* females were taller than males, though in *R. acetosella* the differences between the sexes were less extreme. The size differences between the sexes are not fixed secondary sex characters, since the male and female sizes could change with age or environmental conditions. The late summer correlations between the degree of sexual size dimorphism and sex ratios were significantly positive in *R. acetosa* and *R. acetosella*, though the data on *R. acetosa* is limited. The interactions between the degree of sexual size dimorphism, various soil characteristics and density were found negligible. Contrary to these results, Conn (1980, 1981) discovered in *R. hastatulus* that the height difference between males and females decreases with increasing population density. Females appeared to be more greatly affected by crowding, possibly because of higher energy requirements for setting seed. Moreover, the differences in anthesis date between the sexes increase as density increases and as the content of nitrogen, phosphorus and potassium in soil decreases (Conn 1980, 1981).

Three major hypotheses have been proposed to explain the evolution of sexual dimorphism in body size and morphology of animals (for a review, see Hedrick and Temeles 1989). These hypotheses, reproductive role division, intersexual resource competition and sexual selection, can be applied to plants as well. Most studies on sexual dimorphism in plants have concentrated on reproductive role division or ecological differences. Recently some researchers have also suggested the possibility of sexual selection in plants (see Lovett Doust and Lovett Doust 1988). Lande (1980) assumes in his model that the genetic basis for sexual dimorphism is polygenetic. He demonstrated that sexual dimorphism can evolve if selection acts on the two sexes in opposite ways and if the genetic correlation between the sexes is less than 1.0.

The idea that sexual dimorphism could evolve because of adaptive ecological differences between the sexes has often been dismissed as lacking general applicability. As Shine (1989) reviews, the reason for this dismissal is not contradictory data as much as difficulties in testing the hypothesis. Slatkin (1984) has examined the ecological basis of sexual dimorphism and has concluded that there are three ecological mechanisms that could account for the origin of sexual dimorphism: First, ecological conditions could favor different ecological roles for the two sexes (dimorphic niches). Second, ecological conditions could favor two distinct types of individuals of either sex (bimodal niches). Third, ecological conditions could favor dimorphism through competition for limited resources, analogous to ecological character displacement.

The observed positive correlations between the degree of sexual size dimorphism and sex ratio in both *R. acetosa* and *R. acetosella* show that the females are more abundant in populations where females are larger. As observed by Korpelainen (1991), the major cause of biased sex ratios in *R. acetosella* is different mortality between the sexes, and mortality may be an important factor leading to biased sex ratios in *R. acetosa* as well. On the other hand, intraspecific competition and differences in vegetative vigour between the sexes have a minor effect on the sex ratios (Korpelainen 1991). I propose that the reason for sexual size dimorphism in *Rumex* is an ecological mechanism which does not operate through competition between the sexes but rather through the interaction between mortality differences and size distribution. If competition between the sexes were to cause the observed sexual size dimorphism, the increased level of dimorphism should result in more equal sex ratios due to a reduced level of between-sex competition – exactly the opposite of the results in this study. Putwain and Harper (1972) have shown that in *R. acetosella* females allocate between three to four times more of their biomass to sexual reproduction than do males. With increasing size, females gain proportionately more in terms of viability than do males and the sex ratios become more female-biased. A cause for the decreased size difference and for the somewhat greater female predominance by late summer may be an event where the smallest males suffer from greater mortality and perish during the summer. In summary, size differences between the sexes in *R. acetosa* and *R. acetosella* are based on the interaction between mortality differences and size distribution. Taller plants have lower mortality, and this feature is more important for females which have higher resource demands in reproduction than do males.

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References

Ågren J. 1987. Intersexual differences in phenology and damage by herbivores and pathogens in dioecious *Rubus chamaemorus*L. Oecologia 72: 161–169.

Bawa K. S., Keegan C. R. and Voss R. H. 1982. Sexual dimorphism in *Aralia nudicaulis* L. (Araliaceae). Evolution 36: 371–378.

Bull J. J. 1987. Evolution of phenotypic variance. Evolution 41: 303–315.

Bullock S. and Bawa K. S. 1981. Sexual dimorphism and the annual flowering pattern in *Jacaratia dolichaula* (D. Smith) Woodson (Caricaceae) in a Costa Rican rain forest. Ecology 62: 1491–1504.

Conn J. S. 1980. Patterns of dioecism in the Carolina flora, between sex differentiation and female-biased ratios in *Rumex hastatulus* Baldwin ex Ell. Ph.D.-thesis, North Carolina State University, Raleigh, N.C.

Conn J. S. 1981. Phenological differentiation between the sexes of *Rumex hastatulus*: Niche partitioning or different optimal reproductive strategies? Bull. Torr. Bot Club 108: 374–378.

Farris M. A. and Schaal B. A. 1983. Morphological and genetic variation in ecologically central and marginal populations of *Rumex acetosella* L. (Polygonaceae). Am. J. Bot. 70: 246–255.

Freeman D. C., Klikoff L. G. and Harper K. T. 1976. Differential resource utilization by the sexes of dioecious plants. Science 193: 597–599.

Grant M. C. and Mitton J. B. 1979. Elevational gradients in adult sex ratios and sexual differentiation in vegetative growth rates of *Populus tremuloides* Michx. Evolution 33: 914–918.

Harris W. 1970. Yield and habit of New Zealand populations of *Rumex acetosella* at three altitudes in Canterbury. N. Z. J. Bot. 8: 114–131.

Hedrick A. V. and Temeles E. J. 1989. The evolution of sexual dimorphism in animals: Hypotheses and tests. TREE 4: 136–138.

Korpelainen H. 1991. Sex ratio variation and spatial segregation of the sexes in populations of *Rumex acetosa* and *R. acetosella*. Plant Syst. Evol. 174: 183–195.

Lande R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution 34: 292–305.

Lloyd D. G. and Webb C. J. 1977. Secondary sex characters in plants. Bot. Rev. 43: 177–216.

Lovett Doust J. and Lovett Doust L. 1988. Sociobiology of plants: An emerging synthesis. In: Lovett Doust J. and Lovett Doust L. (eds.), Plant reproductive biology. Oxford University Press, New York, pp. 5–29.

Meagher T. R. 1984. Sexual dimorphism and ecological differentiation of male and female plants. Ann. Missouri Bot. Gard. 71: 254–264.

Onyekwelu S. S. and Harper J. L. 1979. Sex ratio and niche differentiation in spinach (*Spinacia oleracea* L.). Nature 282: 609–611.

Putwain P. D. and Harper J. L. 1972. Studies in the dynamics of plant populations. V. Mechanisms governing the sex ratio in *Rumex acetosa* and *R. acetosella*. J. Ecol. 60: 113–129.

Putwain P. D., Machin D. and Harper J. L. 1968. Studies in the dynamics of plant populations. II. Components and regulation of a natural population of *Rumex acetosella* L. J. Ecol. 56: 421–431.

Schlichting C. D. 1986. The evolution of phenotypic plasticity in plants. Ann. Rev. Ecol. Syst. 17: 667–693.

Shine R. 1989. Ecological causes for the evolution of sexual dimorphism: A review of the evidence. Q. Rev. Biol. 64: 419–461.

Slatkin M. 1984. Ecological causes of sexual dimorphism. Evolution 38: 622–630.

Sokal R. R. and Brauman C. A. 1980. Significance tests for coefficients of variation and variability profiles. Syst. Zool. 29: 50–66.

Sokal R. R. and Rohlf F. J. 1987. Introduction to biostatistics. W. H. Freeman & Co., New York.

Steel R. G. D. and Torrie J. H. 1980. Principles nad procedures of statistics. McGraw-Hill, New York.

Vitale J. J. and Freeman D. C. 1986. Partial niche separation in *Spinacia oleracea* L.: An examination of reproductive allocation. Evolution 40: 426–430.

Wallace C. S. and Rundel P. W. 1979. Sexual dimorphism and resource allocation in male and female shrubs of *Simmondsia chinensis*. Oecologia 44: 34–39.

Westergaard M. 1958. The mechanism of sex-determination in dioecious flowering plants. Adv. Gen. 9: 217–281.